UNIVERSIDADE FEDERAL DO ESPÍRITO SANTO

CENTRO DE CIÊNCIAS HUMANAS E NATURAIS

PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS

Muriquis e Onde Habitam

Fatores que interferem na distribuição espacial de grupos sociais na Mata Atlântica fragmentada

Luana D'Avila Centoducatte

Vitória, ES
Fevereiro, 2017

UNIVERSIDADE FEDERAL DO ESPÍRITO SANTO

CENTRO DE CIÊNCIAS HUMANAS E NATURAIS

PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS

Muriquis e Onde Habitam

Fatores que interferem na distribuição espacial de grupos sociais na Mata Atlântica fragmentada

Luana D'Avila Centoducatte

Orientador: Sérgio Lucena Mendes

Tese submetida ao Programa de Pós-Graduação em Ciências Biológicas (Biologia Animal) da Universidade Federal do Espírito Santo como requisito parcial para a obtenção do grau de Doutora em Biologia Animal

Vitória, ES
Fevereiro, 2017

“It’s the questions we can’t answer that teach us the most.
They teach us how to think”
Patrick Rothfuss, The Wise Man’s Fear

AGRADECIMENTOS

Certamente em um dos momentos mais desafiadores da minha vida, é com este trabalho que encerro meus anos de PPGBAN-UFES. Cada pessoa citada sabe (pelo menos parte) do meu caminho para chegar até aqui. E é por isto que, com muita sinceridade, sou grata:

Ao meu orientador Sérgio Lucena Mendes, por extensas discussões sobre Ciência e suas contribuições para o mundo. Por muitas vezes nossas reuniões se transformavam em complexas discussões sobre a vida, o universo e tudo mais (*Don't Panic!*) que me davam a serenidade de que este trabalho seria concluído.

À Dra. Karen Strier, não só pela vasta contribuição científica para este trabalho e para minha formação, mas também por me receber em seu laboratório e tornar minha estadia em UW-Madison tão amigável e produtiva.

Ao Francisco "Chicó" Barreto, amigo, parceiro, fundamental para conclusão deste trabalho. A pessoa que colocou números, matrizes e Torus nas minhas ideias, o *command center* da minha modelagem.

À (agora) doutora e professora Maria Otávia Crepaldi, pela amizade, parceria e horas e horas de bate papo durantes nossos doutorados.

Ao Rogério Ribeiro, peça chave do Projeto Muriqui – ES, fundamental pra execução dos trabalhos de campo e responsável pelos quase 15 anos de coleta de dados dos muriquis de Santa Maria de Jetibá.

Ao prof. Fabiano "Bião" de Melo, pelas agradáveis discussões sobre os primatas e sobre a vida, a pessoa que me deu um teto pra morar em Madison.

Ao meu tio Zé Emilio e à Dani, pela leitura deste manuscrito e suas valiosas contribuições.

Aos colegas do Laboratório de Biologia da Conservação de Vertebrados, que compartilharam horas de trabalho, café e ciência ao longo desses 10 anos. Em especial ao André que me forneceu os dados demográficos dos muriquis; aos queridos Carla "Cacs" e Marlon por muito do que sei sobre os muriquis; e à Marina pelas discussões sobre ecologia da paisagem e contribuições no capitulo 1.

Às colegas de UW-Madison pelo agradável ano em que passei em Madison e pelos enriquecedores Bioanthro meetings semanais.

Aos meus amigos-padrinhos Ivna e Luciano, que compartilham dos meus dilemas e das minhas alegrias há mais de 20 anos. Mais tempo de vida com eles do que sem eles!

Ao Igor, meu agradecimento mais profundo. Incondicionalmente ao meu lado, sempre me dando forças para seguir em frente e atingir meus objetivos. Me mostrou que independente da distância (seja ela mil ou 9 mil km), somos uma família!

Ao meu pai e minha mãe, pessoas mais éticas que conheço, gratidão eterna por me criarem com liberdade para criticar, questionar, investigar e por me incentivarem a sempre seguir o meu próprio caminho.

Forneceram suporte financeiro para esta pesquisa: CAPES, com concessão da bolsa de doutorado; Programa CSF CAPES/CNPq, com concessão da bolsa SWD; FUNBIO, The MBZ Species Conservation Fund, Fundação Grupo Boticário e Programa PVE CAPES/CNPq, com financiamento do Projeto Muriqui – ES. Forneceram apoio as instituições: UFES, UW-Madison, INMA e IPEMA.

SUMÁRIO

LISTA DE TABELAS

LISTA DE FIGURAS

RESUMO

Em um mundo de paisagens naturais altamente fragmentadas, é conveniente identificar diferentes tipos de comportamento de movimentação animal e como eles contribuem para a compreensão dos processos de dispersão e distribuição de espécies. A demanda por produtos agrícolas cria novos padrões de uso da terra e influencia as taxas de desmatamento, alterando a conectividade entre os habitats, o grau de isolamento e o fluxo genético entre populações, influenciando, portanto, a persistência das espécies na paisagem. Neste contexto, esta tese abordou hipóteses sobre como as características do habitat afetam a distribuição e a movimentação dos muriquis, um primata endêmico criticamente ameaçado, em uma região de Mata Atlântica. Usando dados coletados em campo, teoria dos grafos e modelos espacialmente explícitos baseados no indivíduo, foi possível analisar a resposta populacional de muriquis às variáveis da paisagem, fazer inferências sobre distribuição de grupos sociais, movimentação animal e crescimento populacional e sugerir estratégias de conservação que podem ser implementadas na região. Dados mostram que, de 1970 a 2008, a cobertura florestal aumentou quase três vezes. O número de fragmentos florestais diminuiu mas o tamanho aumentou, refletindo uma regeneração natural que conectou alguns dos fragmentos que se encontravam isolados no passado. O tamanho do fragmento, a conectividade e o crescimento florestal foram identificados como fatores que influenciaram a distribuição de muriquis e a sua persistência na paisagem que, provavelmente, foi assegurada pela regeneração da floresta e pela sua habilidade em explorar florestas secundárias. Dados empíricos mostraram que, em fragmentos florestais isolados, houve uma mudança completa do comportamento esperado de muriquis, que apresenta um padrão onde somente fêmeas dispersam. Pelo menos cinco fêmeas permaneceram em seu grupo natal e se tornaram sexualmente ativas, enquanto outras deixaram o grupo e tornaram-se solitárias. Em fragmentos florestais funcionalmente conectados, o comportamento esperado foi preservado, com dispersão de fêmeas entre grupos. Além disso, foi relatada a fissão de um grupo em dois grupos sociais diferentes, em que o menor migrou para outro fragmento cruzando uma estrada e uma plantação de eucalipto. O modelo MPSG (*Muriqui Population Spread and Growth*), desenvolvido para simular o comportamento de movimentação dos muriquis pela paisagem, utilizou dados de dinâmica populacional como um regulador dos eventos de migração. A simulação resultou em um aumento populacional médio de 2,4 vezes nos próximos 50 anos, com a migração das fêmeas desempenhando um papel importante nesse crescimento populacional. Entretanto, mais de 60% das fêmeas provavelmente não terão sucesso em encontrar um parceiro reprodutivo porque a dispersão pode levá-las a fragmentos sem grupos sociais de muriquis. Verificou-se que, para espécies que apresentam processo de dispersão como os muriquis, a conectividade pode ser tão importante quanto o tamanho do habitat. Para fins de conservação, propomos incrementar a conectividade entre os fragmentos florestais, estabelecer um corredor protegido de biodiversidade e translocar fêmeas jovens para outros grupos sociais da mesma região. Este estudo demonstra a importância de análises históricas da paisagem para compreender o potencial de recuperação de populações de espécies ameaçadas de extinção. Modelos que estimam o comportamento de indivíduos, incluindo informações espaciais e populacionais, podem ser uma poderosa ferramenta para entender como as características da paisagem no passado moldaram a distribuição das espécies no presente e projetar a persistência dessa espécie no futuro.

Palavras-chave: *Brachyteles hypoxanthus*; conectividade de habitat; heterogeneidade da paisagem; regeneração florestal; dispersão; modelos baseados no indivíduo.

ABSTRACT

In a world of highly fragmented natural landscapes, it is convenient to identify different types of animal movement behavior and how they contribute to the understanding of dispersal processes and species distribution. Regional demand for agricultural products creates new patterns of land use and influences deforestation rates, changing the connectivity between habitats and therefore the degree to which animal populations are isolated or can maintain gene flow, and influencing the persistence of species in the landscape. In this context, this thesis addressed hypotheses about how habitat features affect the distribution and movement of the northern muriqui, an endemic, critically endangered primate, in an Atlantic Forest region, a hotspot of biodiversity. Using field-collected data, graph theory and individual-based spatially explicit models, we were able to analyze the muriqui's population response to landscape variables, make inferences about the distribution of social groups, animal movement and population growth, and suggest conservation strategies that can be implemented in the region. We found that from 1970 to 2008, forest cover increased almost three-fold. The number of forest patches is diminished but the size increased, a reflection of the natural regeneration that connected some of the previously isolated patches. We found that patch size, connectivity and forest growth influence the distribution of muriquis, and their persistence in the landscape was probably ensured by forest regeneration and their ability to explore secondary forests. Empirical data showed that isolated forest patches produced a complete change of the typical behavior of muriquis, a primate with female-biased dispersal pattern. At least five females stayed in their natal group and became sexually active and reproductive, while others left the group and became solitary. Forest patches functionally connected preserved that typical behavior, with dispersal of females from one group into another. Other than the expected female dispersal, we also recorded a fission of one group into two different social groups, in which the smallest one migrated to another fragment by crossing a road and an eucalyptus plantation. We developed the MPSG model (Muriqui Population Spread and Growth), which simulates movement behavior across the landscape by using population dynamics outputs as a trigger to regulate the events of migration. The simulation resulted in an average population increase of 2.4-fold in 50 years, with female migration playing an important role in that growth. More than 60% of females will probably have no success in finding a mating partner because their dispersal will lead to empty patches. We found that, for species with dispersal process such as the muriquis, connectivity may be as important as (or even more important than) habitat size. For conservation purposes, we proposed to improve the connectivity between patches, to establish a protected corridor of biodiversity, and the translocation of young females to other groups within the landscape. This study shows the importance of historical landscape analyses to understand potential population recovery of endangered species. Models that estimate the spatial behavior of populations in the landscape using spatial and population information can be a powerful tool to understand how past landscape features shaped present species distribution and to project the future persistence of this species.

Key words: *Brachyteles hypoxanthus*; habitat connectivity; landscape heterogeneity; forest regeneration; female-biased dispersal; agent-based model

APRESENTAÇÃO

O fenômeno mundial de perda e fragmentação de habitat é, certamente, a maior ameaça à nossa biodiversidade. São inúmeras as evidências de que a fragmentação altera a distribuição das espécies e reduz a biodiversidade local. Em paisagens fragmentadas, as espécies que antes se distribuíam de forma contínua, sobrevivem em manchas remanescentes de habitat, isoladas umas das outras. A movimentação animal, seja para buscas diárias de alimento ou parceiros sexuais, seja para eventos de dispersão, também é fortemente alterada, já que há menos conexões entre os remanescentes de habitat. Apesar do desenvolvimento de vários trabalhos teóricos que buscam prever como essas espécies e o ambiente se comportarão no futuro, o destino de ambos é incerto.

Neste contexto, os três capítulos desta tese abordam hipóteses de como as alterações no habitat afetam a distribuição e movimentação das espécies, utilizando como área de estudo uma região de Mata Atlântica, um *hotspot* de biodiversidade (áreas com grande riqueza de espécies, alto grau de endemismo e sob forte ameaça), e como espécie alvo o muriqui-do-norte, um primata endêmico criticamente em perigo de extinção.

Figura A. 1. Fotografia aérea de fragmentos de Mata Atlântica no município de Santa Maria de Jetibá, ES.

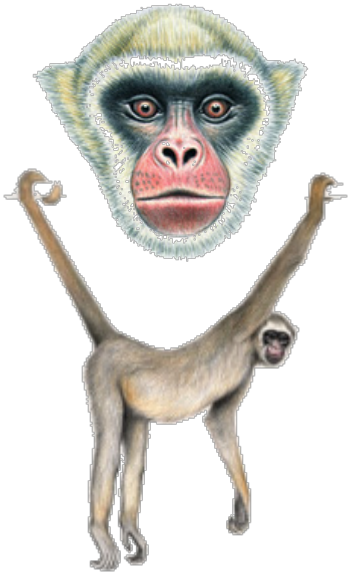


Figura A. 2. Ilustração do muriqui-do-norte, por Stephen Nash.

A Mata Atlântica sofre impactos de atividades humanas há milhares de anos, mesmo antes da colonização portuguesa, com a ocupação de povos indígenas. Porém, a exploração de recursos e a implantação da agricultura pelos europeus intensificaram e aceleraram o processo de desmatamento, chegando ao limite crítico de menos de 12% de sua cobertura original. Atualmente, mesmo com a tendência de redução de cobertura florestal, tem-se observado que vários pontos de Mata Atlântica estão em processo de regeneração, formando um mosaico de florestas secundárias. Consequentemente, os estudos em biologia da conservação sofreram uma mudança de paradigma, com o aumento substancioso do número de trabalhos que investigam a resiliência florestal e a capacidade das espécies de se restabelecerem em florestas secundárias.

O muriqui é um primata arborícola estritamente florestal, e por isso depende da Mata Atlântica para não extinguir-se. É um animal grande e emblemático, que pode atuar como uma espécie bandeira para a conservação da biodiversidade da Mata Atlântica. As

populações de muriquis sofreram intenso declínio em tempos históricos, podem ter atingido valores críticos de densidade e, portanto, são instáveis e propensas à extinção. Resultados de simulações de viabilidade populacional sugerem que os grupos tendem à extinção em algumas décadas se não houver nenhuma estratégia prática de conservação para aumentar a conectividade das florestas em que vivem.

Encontrar dados biológicos e ambientais para realizar o tipo de análise abordado nesta tese não é fácil. Entretanto, esses dados existem para a região de Santa Maria de Jetibá (SMJ), ES, e para os grupos de muriquis que habitam fragmentos florestais nesse município. A área estudada proporciona um ambiente adequado para testar efeitos das alterações da paisagem na ocorrência de espécies, uma vez que, atualmente, a caça de primatas é pouco frequente na região e, por isso, a distribuição dos grupos é influenciada majoritariamente por perda (ou ganho) de habitat e fragmentação. Além disso, em SMJ, os muriquis são continuamente monitorados desde 2002, com a criação do Projeto Muriqui – ES. Ao longo dos últimos 15 anos, foram realizados avanços tanto no conhecimento da dieta e comportamento dos muriquis quanto na obtenção de informações sobre demografia e distribuição das populações no Espírito Santo.

Os resultados desta tese extrapolam a pesquisa científica e possuem grande importância para ações de conservação dos muriquis previstas no "Plano de Ação Nacional para a Conservação dos Muriquis", elaborado sob a coordenação do ICMBio/MMA e no "Plano de Ação Estadual para a Conservação dos Muriquis no Espírito Santo" elaborado sob coordenação do IEMA/SEAMA. Contribuem para a identificação de fragmentos adequados para sobrevivência de grupos de muriquis, pontos críticos de conexão entre estes fragmentos e o que podemos prever para a persistência da espécie no futuro.

Estrutura da tese

Esta tese foi escrita em três capítulos em formato de artigo científico.

No capítulo 1, investigamos a relação entre a ocorrência de muriquis e variáveis da paisagem, através da quantificação de mudanças na estrutura da paisagem ao longo do tempo (1970-2008) em termos de tamanho, forma e conectividade dos fragmentos florestais. Usando teoria dos grafos e as análises em nível de paisagem fomos capazes de identificar habitats adequados para muriquis e avaliar o que as mudanças na cobertura florestal podem nos informar sobre os processos históricos e como eles afetam a distribuição da população atual e a persistência dos muriquis. Testamos as seguintes hipóteses sobre quais fatores seriam limitantes para ocorrências de muriquis: (1) se a quantidade de floresta é o único fator limitante, os muriquis estão amplamente distribuídos em fragmentos florestais adequados em termos de área; (2) se a perda e fragmentação históricas de habitat também atuam como fatores limitantes, os muriquis estão distribuídos em fragmentos que apresentam não só área adequada, como também conectividade com outros fragmentos florestais.

Os principais resultados deste capítulo foram: (1) Houve um expressivo aumento na cobertura florestal desde 1970, com balanço positivo entre desmatamento e regeneração. De 1970 a 2008 a cobertura florestal aumentou quase 150%. Apesar da diminuição do número de fragmentos florestais, houve incremento de área, o que reflete a conexão de fragmentos previamente isolados por regeneração natural. (2) Tamanho do fragmento,

conectividade e crescimento florestal influenciaram a distribuição de muriquis. Somente 27 fragmentos, de um total de 1598 mapeados para 2008, foram identificados como adequados em termos de tamanho e 13 foram adequados em termos de área e fluxo potencial entre populações. Entretanto, alguns desses fragmentos não apresentaram ocorrência da espécie. (3) 12 das 13 populações de muriquis foram encontradas em remanescentes florestais que já existiam em 1970, que persistiram onde o crescimento florestal foi maior.

O processo intenso de desmatamento provavelmente impactou negativamente a abundância de muriquis, mas sua persistência foi garantida pela regeneração florestal e pela habilidade da espécie em explorar florestas secundárias, consistente com observações feitas por pesquisadores com outras populações de muriquis. Este capítulo demonstra a importância das análises históricas de paisagem na compreensão da distribuição atual de espécies, além de seu potencial para recuperação populacional de espécies ameaçadas de extinção.

No capítulo 2, apresentamos observações empíricas de campo que incluem a dispersão de fêmeas em cinco grupos de muriquis, além da fissão de um grupo e movimentação do novo grupo entre diferentes fragmentos florestais, para colonização de uma nova área. Além disso, utilizando dados de história de vida das fêmeas de muriquis, dados de movimentação entre fragmentos florestais e dados espaciais (obtidos no capítulo 1), levantamos hipóteses sobre como a fragmentação florestal pode afetar o comportamento de dispersão e movimentação, além de sugerir implicações para o manejo do habitat e estratégias de conservação desta espécie.

O resumo dos eventos de movimentação, juntamente com os dados de conectividade do habitat, forneceu uma linha de base para o desenvolvimento de um mapa conceitual para prever o comportamento de movimento de muriquis em uma paisagem fragmentada. Em fragmentos isolados, o comportamento típico de fêmeas de muriquis, de dispersar na puberdade, é completamente alterado, com as fêmeas permanecendo em seu grupo natal ou tornando-se solitárias. As migrações são quase inexistentes e o movimento é restrito ao próprio fragmento. Em fragmentos com maiores índices de conectividade, o comportamento de dispersão é mantido e eventuais movimentações entre diferentes fragmentos florestais podem ocorrer. Em uma situação intermediária, com conectividade parcial, a decisão de dispersar parece ocorrer em nível individual e podem ocorrer eventos de migração esporádicos.

Um desafio importante no manejo de populações de animais silvestres é compreender os padrões de mudanças de habitat ao longo do tempo. Por outro lado, a conectividade de habitat e o fluxo entre grupos sociais são fatores essenciais para assegurar a viabilidade da população de muriquis. Assim, reconhecemos a importância de três estratégias de conservação que poderiam ser implementadas na região de SMJ: (1) assegurar a conectividade entre os fragmentos florestais; (2) estabelecer um corredor de proteção da biodiversidade; e (3) translocar as fêmeas entre grupos sociais em SMJ.

No capítulo 3, desenvolvemos e implementamos o *MPSG model* (*Muriqui Population Spread and Growth*), um modelo espacialmente explícito baseado no indivíduo, que incorpora a dinâmica populacional de muriquis e avalia, por meio de simulações, a importância das características da paisagem para a movimentação dos muriquis e o crescimento populacional. Ao combinar abordagens diferentes – um modelo espacialmente explícito com um modelo de dinâmica populacional – foi

possível estimar as seguintes respostas populacionais em um intervalo de tempo de 50 anos: (1) o número de dispersões bem-sucedidas; (2) estimativas de tamanho da população para cada grupo (3) importância da migração para a dinâmica populacional de cada grupo; e (4) importância relativa de cada fragmento florestal (e respectivos grupos sociais) no fornecimento de indivíduos para outros fragmentos na paisagem.

Os principais resultados deste capítulo foram: (1) a população crescerá 2,4 vezes em 50 anos e as migrações desempenharão um importante papel neste crescimento; (2) o grupo da Mata do Belém está completamente isolado dos outros grupos sociais em Santa Maria de Jetibá; (3) mais de 60% das fêmeas que dispersarem provavelmente não terão sucesso reprodutivo, pois não encontrarão outros grupos sociais e se estabelecerão em fragmentos florestais sem grupos sociais; e (4) a conectividade pode ser tão importante quanto (ou mesmo mais importante que) o tamanho do habitat para a persistência dos muriquis na paisagem.

Nossa simulação sugere que os grupos sociais de muriquis em SMJ são organizados como uma população espacialmente estruturada, composta por fragmentos florestais que mantêm grupos sociais locais, interconectados por indivíduos que dispersam entre eles. Esta dinâmica é o resultado de processos ao nível dos indivíduos. O sistema em SMJ apresenta tanto propriedades de metapopulação quanto dinâmica *source-sink*. No entanto, ainda faltam dados explícitos para consolidar ambas as hipóteses.

Um número significativo de modelos vêm sendo desenvolvidos para compreender o processo de fragmentação e seus efeitos na persistência das espécies. O uso de modelos populacionais como complementos aos modelos de habitat vem sendo incorporado ao planejamento de ações de conservação, auxiliando nas previsões de respostas demográficas espécie-específicas às mudanças ambientais. Acreditamos que o manejo apropriado dos habitats, com o aumento da cobertura florestal e da conectividade entre eles, seria capaz de mitigar os efeitos da fragmentação na distribuição de muriquis e, provavelmente, na da maior parte da biodiversidade local.

Capítulo 1

Efeitos da Regeneração Florestal na Distribuição Espacial de um Primata Criticamente em Perigo de Extinção

---

Effects of Atlantic Forest Regeneration on the Spatial Distribution of a Critically Endangered Primate

Introduction

The major threats to species facing extinction are habitat loss and fragmentation (Groombridge 1992; Sala et al. 2000; Tabarelli and Gascon 2005). This phenomenon occurs throughout the world, especially in tropical forests (Skole and Tucker 1993), where fragmentation means potential loss of biological diversity, since they have complex ecological structure, high species diversity and endemism (Wilcove et al. 1986).

Global, national and regional demand for agricultural products create new patterns of land use and influence rates of deforestation (Fearnside 2008; Freitas et al. 2010; Laurance et al. 2014), changing the connectivity between habitats and therefore the degree to which animal populations are isolated or can maintain gene flow (Frankham 2007) and influencing the persistence of species in the natural landscape (Taylor et al. 1993). Often, species that in the past were distributed continuously in the landscape survive in the remaining patches of habitat, isolated from each other by a highly modified or degraded matrix (Debinski and Holt 2000; Fahrig 2003). Until early 2000's, it was unclear which main factors were responsible for influencing the distribution of populations in fragmented landscapes (Debinski and Holt 2000). However, during the last decade, scientists have been making efforts in ascertaining variables that could predict the occurrence of the species. The degree to which fragmentation represents a barrier in population distribution varies according to life history strategies of different species (e.g. invertebrates (Watts et al. 2016); birds (Ferraz et al. 2007), mammals (Li et al. 2015). Arboreal mammals, including primates, are particularly sensitive to habitat disturbances (Chiarello and de Melo 2001; Keesen et al. 2017).

According to the Theory of Island Biogeography (MacArthur and Wilson 1967) species richness in forest fragments should be strongly dependent on patch size and degree of isolation. Reducing the size of forest fragments causes increased edge effects and reduced availability of resources, making species with larger space requirements more susceptible to extinction in small fragments (Murcia 1995; Fleishman et al. 2002). Increasing the degree of isolation can reduce opportunities for individuals to disperse, resulting in reduced gene flow between populations (Frankham 2007).

Graph theory-based analysis (Pascual-Hortal and Saura 2006) provides a method for evaluating how fragment size and landscape-level descriptors, such as connectivity between fragments, affect the availability of habitat for a species. Specifically, it takes into account how the distance between patches relative to the distance that a species can disperse affects isolation; thus requiring access to data on landscape structure (Fischer and Lindenmayer 2007) and knowledge of the movement capacity of a species. Habitat patches are represented by nodes, which possess certain attributes (such as patch area). Connections between two nodes represent a functional connection, indicating that an organism is able to move from one patch to another over an area of "non-habitat". Nodes can be connected to other nodes or completely isolated; the corresponding graphs are constructed to represent the functional connectivity of the landscape (Pascual-Hortal and Saura 2006).

Finding available landscape and biological data to perform this type of analysis is not easy. However, such data are available for some field sites at the southeast region of the Brazilian Atlantic forest, a biodiversity "hotspot" (Myers 2000; Jenkins et al. 2013) that supports one of the most critically endangered primates in the world, the northern muriqui, *Brachyteles hypoxanthus* (Primates, Atelidae) (Mittermeier et al. 2006). The

Brazilian Atlantic Forest decreased by more than 88% of its original forest cover (SOS Mata Atlântica/INPE 2014), mainly due to resource exploitation and implementation of agriculture. Most of the remaining Atlantic Forest is represented by fragments smaller than 100 ha (Ribeiro et al. 2009), composed of secondary forests (Metzger 2000). Even original forest cover was selectively logged in the past (Dean 1996). The extinction of muriquis in much of their historical distribution is mainly due to the destruction of forests (Aguirre 1971; Mittermeier et al. 1987). Currently, most of the muriquis populations are at low population densities, distributed in small forest fragments (Strier 1993/1994; Mendes et al. 2005).

In the municipality of Santa Maria de Jetibá (SMJ), this species have been continuously monitored since 2002 by researchers of the Muriqui Project – ES. The muriquis are distributed in 13 forest fragments no bigger than 350 ha, in addition to 11 other fragments in which we suspect they might occur. All groups of muriquis in SMJ sum about 120 individuals (updated from Mendes et al. 2005). The study area covered in this paper provides a good environment to test different predictors of occurrence of species in fragmented landscapes. Since primate poaching is currently uncommon (Mendes et al. 2005), species distribution is mainly influenced by habitat loss and fragmentation.

So, if the only thing limiting muriqui occurrence today is forest, then we expect to find them widely distributed in forest patches with minimally suitable sizes. However, if muriqui occurrence today reflects historical habitat loss and fragmentation, then we expect to find them spatially restricted to regions with not only suitable-size forest patches but also with high connectivity among patches. We investigated the relation between muriquis occurrence and landscape variables by: (1) investigating the changes in landscape structure over time (1970-2008) in terms of size, shape and connectivity between forest patches; and (2) finding if current occurrence of muriquis in habitat patches are related to landscape variables (patch's spatial characteristics or connectivity with other patches). Using graph theory and landscape-level analyses we were able to identify current suitable habitats for muriquis and to evaluate how quantifying changes in forest cover can inform us about historical processes and how such processes affect present population distribution and species persistence.

Methods

Study site

We conducted this study in Santa Maria de Jetibá (SMJ), a municipality of 735 km^2 in the central-southern mountainous region located approximately 80 km northwest of Vitória, Espírito Santo, Brazil (41^{o}02'W – 40 ^{o}35'W; 19^{o}56'S – 20^{o}13'S; Figure 1.1). It is situated in the phytogeographic domain of montane and submontane Atlantic Forest, with altitudes ranging from 400 to 1,450 meters and a highly sloping relief (Mendes et al.2005). This region presents a very complex landscape, characterized by several small patches of Atlantic forest isolated from each other or partially connected through hilltops and surrounded by different forms of land use and land cover.

The region was colonized by European immigrants, mostly from Pomerania, a region of northern Poland and Germany on the southern shore of the Baltic Sea. They still keep alive the culture of their origin country by preserving their mother tongue, customs and agrarian structure. They established a complex system of small private farms and family agriculture, which constitutes the main economic activity of SMJ, with high diversity of

agricultural production, especially horticulture and aviculture (data provided by the Secretary of Agriculture of SMJ, 2013).

Although the Atlantic Forest in the region has been intensively fragmented in the past, reaching less than 15% of native forest, forests have increased in size during the last four decades. There are currently about 30 to 40% of secondary forest in intermediate to advanced stages of succession (Dos Santos et al. 2012).

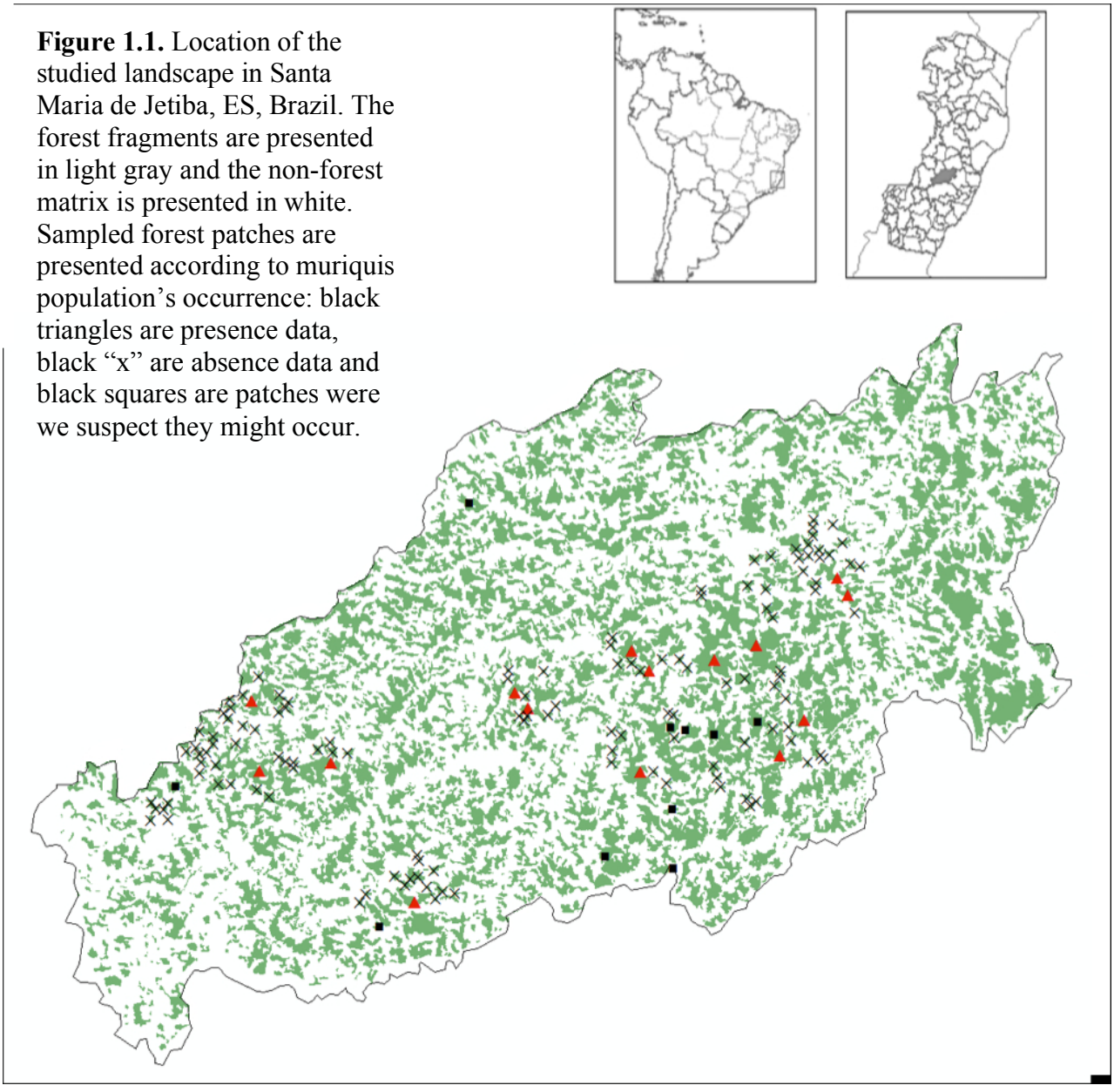


Figure 1.1. Location of the studied landscape in Santa Maria de Jetiba, ES, Brazil. The forest fragments are presented in light gray and the non-forest matrix is presented in white. Sampled forest patches are presented according to muriquis population's occurrence: black triangles are presence data, black "x" are absence data and black squares are patches were we suspect they might occur.

Study species

The northern muriqui, *Brachyteles hypoxanthus* (Primates, Atelidae) is a diurnal and arboreal species, living strictly in forest habitats. Its historic distribution comprises montane forests from southern Bahia State to Espírito Santo State and southern Minas Gerais State, excluding lowland forests (Aguirre 1971). Currently the northern muriquis are found only in some Atlantic Forest remnants in Espírito Santo and Minas Gerais.

Northern muriquis are currently restricted to highly fragmented forest habitats. Also, the females of this species migrate from their natal group when they reach puberty (Printes and Strier 1999; Strier and Ziegler 2000) and they often become solitary when they reach adulthood, probably due to the lack of other social groups in fragmented habitats (Mendes et al. 2005). So, muriquis are presently categorized as a "critically endangered" species by both the IUCN Red List of Threatened Species (IUCN 2013) and the Brazilian list of endangered species (Machado et al. 2008), and also the Espírito Santo State list of threatened fauna (IPEMA 2007).

Species data collection

SMJ is a long-term site of research with muriquis, where we have been collecting data of this species occurrence regularly since 2002. We have been using two different approaches to find evidence of muriquis in the area, one indirect, through interviews with the local population; and one direct, conducting an active search for muriquis populations on the forest patches. For this paper we used data of 146 sampled forest fragments and we considered as presence data only if an individual was sighted by our field researchers.

We used two different methods of interview to get information on the occurrence of muriquis: (1) selection of informants by reference groups, using snowball methodology, i.e., asking informants to recommend knowledgeable people and following their referrals (Davis and Wagner 2003); and (2) interviews conducted with farm owners of the regions surrounding forest fragments. The information on the occurrence of muriquis was obtained through semi-structured questionnaires, complemented by free-ranging interviews and informal conversations (Huntington 2000). When the presence of muriquis was reported during the interviews, trained assistants performed playback experiments in strategic sites and conducted census in forest patches adjacent to these farms to confirm the records.

The census followed the assumptions of the method of Transect Linear Census (Buckland and Elston 1993). Each census was initiated early in the morning (approximately 06:30), which allowed for better location of the species. It lasted all-day and ended late in the afternoon (17:30 - 18:00). Along with trails, the method of viewpoint was also employed. This method consists in searching for primates in strategic points which give us a broad view of a particular valley or hillside. When a muriqui group was located, we recorded the group size and the geographic location using a handheld Global Positioning System receiver (GPS). We also took pictures of each individual in an effort to verify that each of them was not counted multiple times.

Mapping the forest patches

The landscape was characterized using a combination of classifications from aerial photographs from 1970 (Dos Santos et al. 2012) and 2008 (IEMA 2007/2008) (both 1m resolution) and validation of these classifications in the field. The native vegetation was classified following parameters defined by a Brazilian Federal Resolution (CONAMA no10, 1 October 1993): (1) *vegetation at an initial stage of succession*, area with native herbaceous/low size shrubby vegetation, ranging from open to closed cover; (2) *forest at an intermediate stage of succession*, area with native forest with predominantly arboreal vegetation over herbaceous/shrubby, and different strata with emerging individuals; and (3) *forest at an advanced stage of succession*, area with native vegetation at an advanced stage of succession or primary forest, with native forest with predominantly arboreal vegetation over herbaceous/shrubby and closed and relatively uniform canopy. We validated the 2008 data by verifying the land cover of 400 randomly selected locations in the field, allowing us to detect and fix errors in order to obtain a high quality classification of the region. The main source of confusion was between intermediate and mature successional stages; nevertheless, the accuracy was above 90% for all classes, using Kappa index validation.

To characterize the forest configuration in SMJ, we used three spatial characteristics, area (*A*) in hectares, perimeter (*P*) in meters, and shape (*PARA*), or P/A and two connectivity indices, the integral index of connectivity (*IIC*), and the probability of connectivity index (*PC*) derived from graph theory (Pascual-Hortal and Saura 2006; Saura and Pascual-Hortal 2007). Both connectivity indices are calculated from the area of the patches and the distances between them, and take into account the connected area existing within the patches and the estimated dispersal flux between different patches (*IICflux* and *PCflux*) and their contribution as stepping stones or connecting elements that uphold the connectivity between other patches (*IICcon* and *PCcon*). The *IIC* is binary, using topological distances between patches, while *PC* is probabilistic, using maximum product probability. For more information, see Saura and Rubio 2010.

Analyses of temporal changes in forest fragments

As the maps of forest cover from 1970 and 2008 have the same resolution (1m), we avoided biases arising from comparison of aerial photographs from different years. Changes in the amount of forest cover and composition of forest fragments were quantified using ESRI®ArcMap™ 10 software. Our data were not normally distributed, so we used the nonparametric Wilcoxon signed rank test with continuity correction to compare paired samples using R software (R Development Core Team 2016).

Relationships between species occurrence and forest configuration

To evaluate the occurrence of muriquis today, we transformed the 1970 and 2008 forest maps into binary maps of possible habitat and non-habitat classes. As our study species uses secondary and primary forests (Fonseca 1985; Strier 1987a), we considered only those patches classified as being at intermediate or advanced stages of succession as possible habitats. We selected 146 forest patches that represented a wide range of fragment size in SMJ. Forest patches were first selected based on observed and reported knowledge of muriqui present and past occupancy. Then, we extended our survey to

additional vicinity fragments, with different sizes, in order to incorporate a wider range of patch sizes to the analyses.

To set our model, we established (1) a model in which the occurrence of species (response variable) in forest patches could be explained as a function of different sets of explanatory variables and (2) a null model, in which occurrence is a function of a constant parameter and not of any other tested variable. The species presence/absence was modeled statistically using simple logistic regressions through Generalized Linear Models assuming a binomial probability distribution (Jongman et al. 1997; Harrel 2001). We used the patch's spatial characteristics and connectivity indices as explanatory variables. The models were compared and selected according to Akaike's information Criterion (AIC; Burnham and Anderson 2002). Models that presented AIC variation less than 2 ($\Delta AIC<2$) were considered equally plausible models for the data set analyzed. All statistical analyses were performed using R software (R Development Core Team 2016).

In modeling species presence/absence pattern of muriquis, we identified a set of variables that can predict the probability of occurrence of muriquis. We used the median of each regression curve to establish a threshold of suitable patches. Each variable identified as plausible to pinpoint potentially suitable forest habitats for muriqui populations was set as a layer; we then built the intersection of those layers in order to create a unique map of suitable forest patches.

Results

Changes in forest fragments

Mature forest (forest at an intermediate and advanced stage of succession) increased from 10,654 ha (15.5%) to 26,500 ha (36%) of the total area over the 40 years interval between the two mappings (1970 and 2008) (Figure 1.2). The growth of 15,846 ha of mature native forest in the municipality of SMJ corresponds to an increase of almost 150%. The proportion of vegetation at initial stage of succession also increased, from 4,128 ha (5.6%) to 7,435 ha (10.1%), which corresponds to an increase of 3,307 ha (80%).

In 1970 there were 1,598 forest patches with areas ranging from 1 to 229.8 ha, while in 2008, after almost 40 years of landscape changes, there were 1,117 forest patches with areas ranging from 1 to 953.7 ha. The reduction in the number of patches reflects the natural regrowth that connected some of the previously isolated patches. This also contributed to the increase in the size of forest patches in the small and large patches categories, but not of intermediate sized patches (Table 1.1).

Table 1.1. Summary of forest patches in the landscape of Santa Maria de Jetibá, ES, Brazil in 1970 and 2008. Area values are shown in hectares. Values in parentheses are the number of patches (NP).

	1970	**2008**
% patches < 50ha (NP)	98 (1,566)	88.9 (993)
Sum Area of patches <50ha	8,010.80	9,576
% patches 50-100ha (NP)	1.7 (27)	6 (67)
Sum Area of patches 50-100ha	1,815.90	4,535
% patches >100ha (NP)	0.3 (5)	5.1 (57)
Sum Area of patches >100ha	827.3	12,389
% patches total (NP)	100 (1,598)	100 (1,117)
Total Sum Area of patches	10,654	26,500

The results of Wilcoxon test showed that all variables increased over time (Table 1.2). The proportion of forest patches important as stepping stones (*IICcon* and *PCcon*) increased at least 300-fold and the proportion of potential flux (*IICflux* and *PCflux*) among forest patches increased at least 100-fold.

Table 1.2. Results of nonparametric Wilcoxon signed rank test with continuity correction to compare the landscape in 1970 and 2008. All variables showed increased values from 1970 to 2008. *: significant variables ($p<0.05$); W: test values.

Variable	**W**	***p***	**Proportion**
Area	2108	3.289e-10*	2.5
Perimeter	404	2.2e-16*	-
Shape	170	2.1e-16*	-
IIC	519	2.2e-16*	97.6
IICflux	546	2.1e-15*	107.7
IICconn	740	2.0e-16*	309.2
PC	831	2.1e-16*	49.6
PCflux	361	2.599e-16*	107.0
PCconne	437	2.3e-16*	664.6

Characteristics of patches occupied by muriquis

The muriquis were detected in 13 out of 146 sampled patches. Their occurrence was affected by habitat configuration in 2008 (Table 1.3), as weak support was shown for the null model ($\Delta AIC= 60.419$; $p<0.05$). Although almost all explanatory variables can predict the species occurrence in 2008, with the exception of *IICcon* and *PCcon*, three models were found to be equally plausible to explain variation (best models), Shape ($\Delta AIC= 0$), Area ($\Delta AIC= 1.773$) and Perimeter ($\Delta AIC= 0.029$).

Twelve of the 13 patches occupied by muriquis in 2008 were also present in 1970. However, the characteristics of these patches in 1970 did not predict muriqui occurrence (Table 1.3). The smallest suitable forest patch for muriquis presented an area of 170 ha. Only one group of muriquis was distributed in a size-suitable patch in 1970. In 2008, seven were distributed in size-suitable patches and six (out of these seven) of them were

distributed in flux-suitable patches. However, 21 suitable patches were not known to have a muriqui population and six groups were in non-suitable patches.

Patches with larger area, more complex shape and functionally connected with other patches were considered more suitable for muriqui population, while the absence data occurred mostly on smaller patches with less complex shape and isolated from other patches. Stepping stones (*IICcon* and *PCcon)* were considered not suitable for populations, independently of their topological distance to other fragments.

Table 1.3. Comparison of simple models (one explanatory variable) to select the best models explaining the variation in the probability of occurrence of muriquis in fragmented landscapes (n=146). P: significance; *: significant variables (p<0.05); ^{ns}: non-significant variables; β: regression coefficient; Z: test value; AIC: Akaike's coefficient criteria. Both null models were significantly random.

Year	Explanatory variables	β	Z	*p*	AIC	ΔAIC
1970	Area	-1.12E-06	-0.29	0.774 ^{ns}	100.36	14.479
	Perimeter	-4.58E-05	-0.19	0.849 ^{ns}	100.41	14.529
	Shape	20.3614	1.15	0.25 ns	99.103	13.222
	IIC	-1.88E-12	-0.38	0.706 ns	100.24	14.359
	IICflux	-9.32E-13	-0.13	0.897 ^{ns}	100.43	14.549
	IICcon	-4.89E-11	-0.43	0.666 ^{ns}	99.897	14.016
	PC	-1.15E-12	-0.23	0.815 ^{ns}	100.38	14.499
	PCflux	-4.00E-13	-0.07	0.947 ^{ns}	100.45	14.569
	PCcon	-0.00423	-1.49	0.1371 ^{ns}	85.881	0
	null model	-1.7087	-7.54	<0.05 *	130.53	44.649
2008	Area	1.36E-06	3.831	0.000128 *	55.974	1.773
	Perimeter	4.93E-05	3.79	0.000151 *	55.03	0.829
	Shape	-145.944	-2.97	0.00294 *	54.201	0
	IIC	1.07E-14	2.64	0.0083 *	73.731	19.53
	IICflux	2.15E-14	2.658	0.00786 *	72.073	17.872
	IICcon	1.69E-14	1.732	0.0833 ^{ns}	79.26	25.059
	PC	3.55E-14	2.361	0.0182 *	74.263	20.062
	PCflux	6.47E-14	2.348	0.0189 *	76.334	22.133
	PCcon	2.73E-14	0.245	0.807 ^{ns}	81.824	27.623
	null model	-1.8918	0.246	<0.05 *	114.62	60.419

Suitable forest habitat and muriqui populations

We used the seven variables identified as good predictors of muriqui patch occupancy in 2008 (see above) to evaluate the occurrence of other potentially suitable patches for muriquis across the entire SMJ landscape. We found a total of 27 potentially suitable forest patches in terms of area; only 13 of these patches also provided potentially

suitable flux between populations (Figure 1.3). In 1970, only two forest patches were size-suitable for muriqui populations and no patches were identified as flux-suitable.

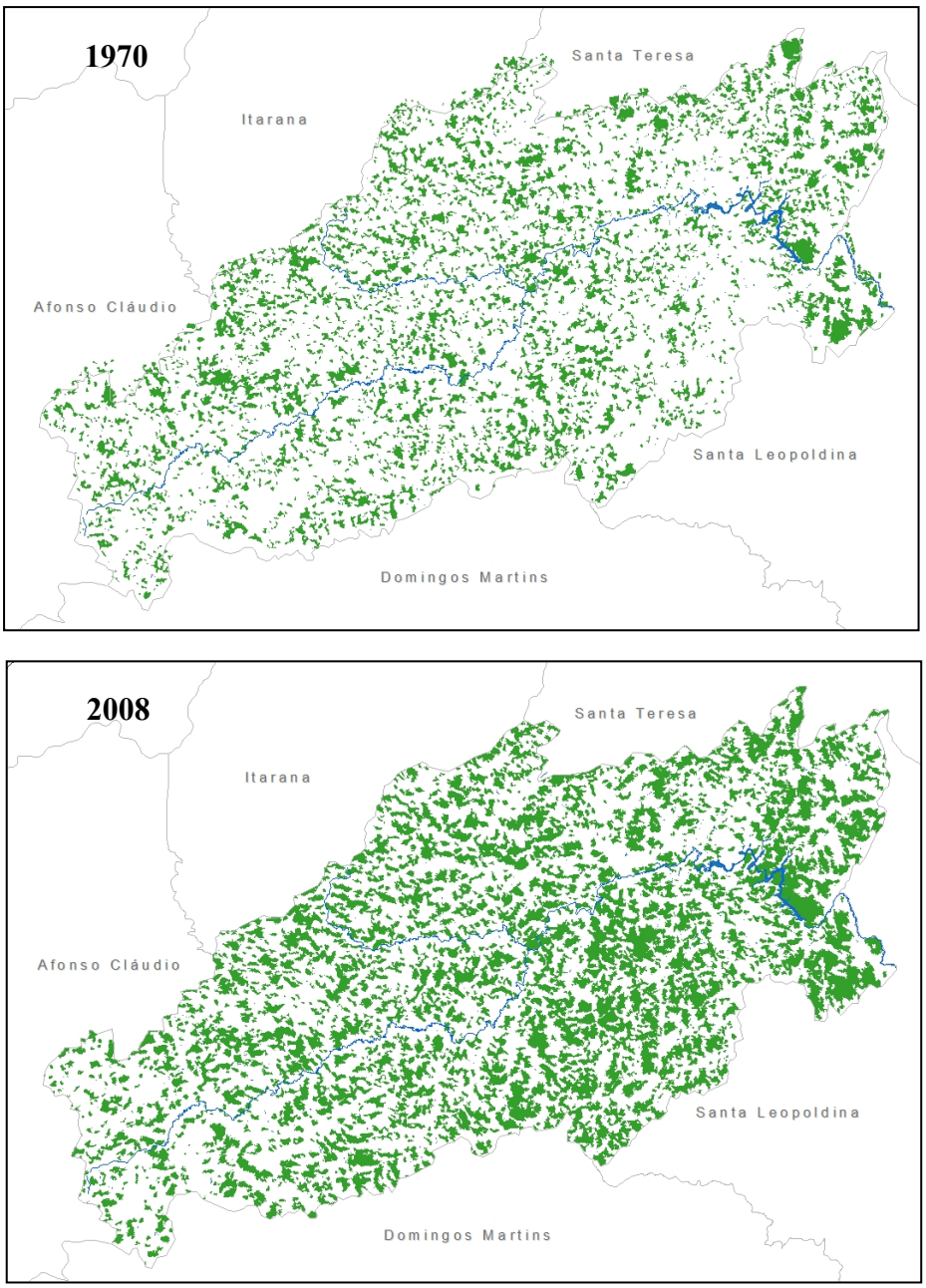


Figure 1.2. Forest cover in 1970 and 2008 in municipally of Santa Maria de Jetibá, ES, Brazil, showing forest growth in 40 years.

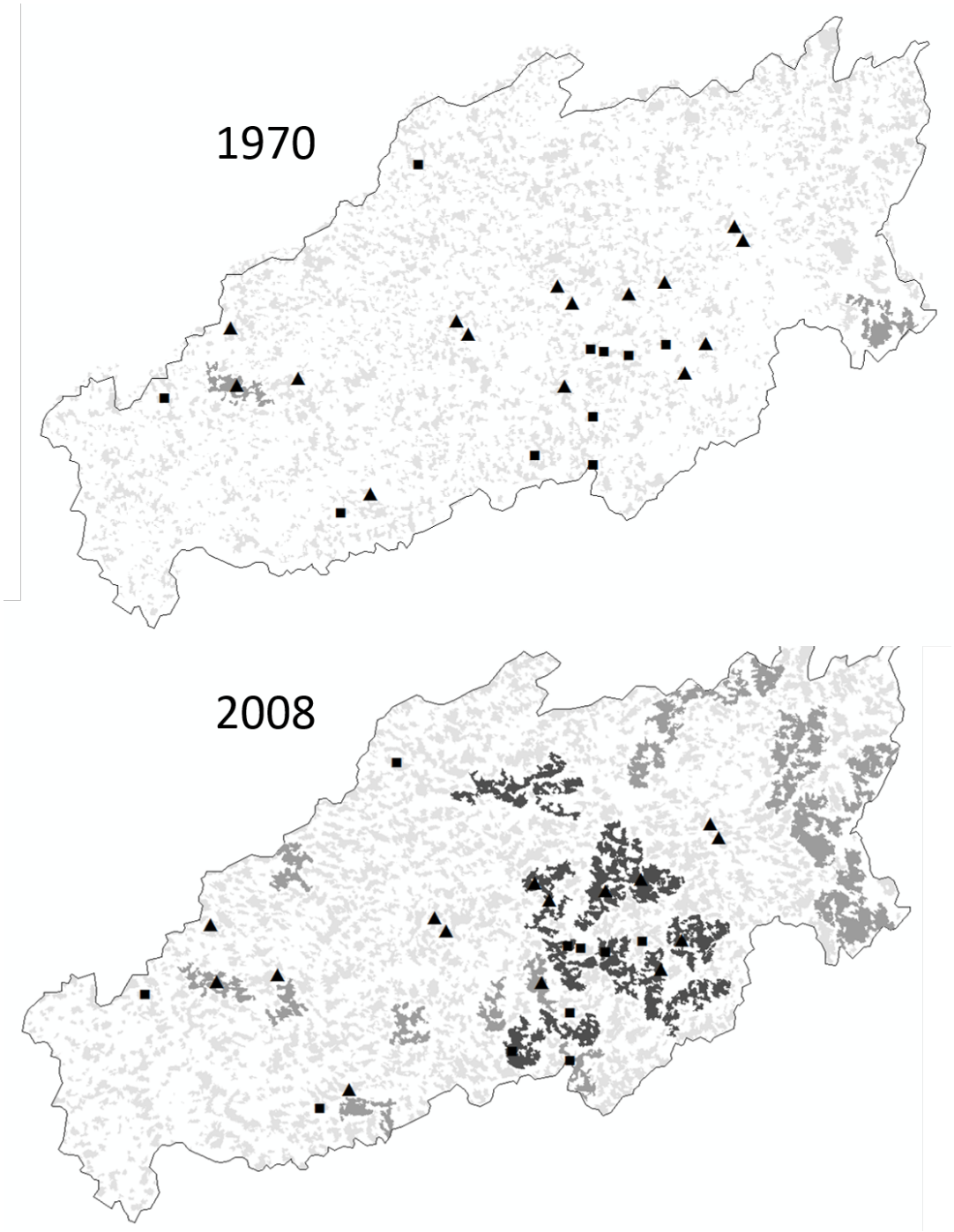


Figure. 1.3 Suitable forest patches for persistence of muriqui populations. The forest fragments presented in light gray are non-suitable, medium gray are size-suitable and dark gray are size and flux-suitable. The non-forest matrix is presented in white. Occurrence of muriquis presented: black triangles confirmed and black squares suspect.

Discussion

We found that: (1) forest cover and connectivity between patches increased remarkably in 40 years; (2) most forest patches are very small, less than 50 ha; (3) small forests play a crucial role as stepping stones, thus reducing patch isolation; (4) no patches were suitable for muriquis in the past and only 13 patches provided both sufficient size and the potential for flux between groups in 2008; and (5) the persistence of muriquis occurred where forest growth was higher.

Changes in forest fragments

Our estimated area of forest patches (36%) in 2008 is larger than the area found by the main study of the Atlantic Forest processes and patterns in Brazil for SMJ (26%) (SOS Mata Atlântica/INPE 2008). It is possible that mapping errors have caused differences between these estimates; however, we believe that the discrepancies observed are more probably due to differences in methodology, related to the criteria used to include small fragments and the spatial resolution of satellite images and aerial photographs. Our field checking provided a high quality map for local analyses. Thus, the difference between both estimates might be that SOS Mata Atlantica Foundation considered only forest fragments >3 ha and used 20m spatial resolution images (SOS Mata Atlântica/INPE 2008), in contrast to the >1 ha forest patch and 1 m spatial resolution used in this study.

The amount of forest found in the studied landscape lies within the known threshold values for species extinction, varying from 30% to 50% of remaining habitat, as proposed by some studies (Fahrig 2002; Pardini et al. 2010; Hanski 2011). The extinction threshold is more likely to affect local dispersers (Liao et al. 2015), so if the forest regeneration trend in SMJ persists for a certain amount of time, it is possible that most of local biodiversity will have ensured minimal conditions to persist in the study area.

The inclusion of smaller forest patches in analyses is particularly relevant in landscapes such as SMJ, as small fragments are definitely the largest fraction of the number of patches (88.9% with <50 ha in 2008) and as they improve connectivity among larger patches. Other studies of size distribution of Atlantic Forest fragments have also shown that most patches are smaller than 50 ha (Ranta et al. 1998; Ribeiro 2009; SOS Mata Atlântica/INPE 2015). Furthermore, small patches can function as stepping stones for animal movement across the landscape (Sekercioglu et al. 2006; Castellón and Sieving 2007; Uezu et al., 2008), allowing species survival in a mosaic of forest fragments (Martensen et al. 2008).

Forest cover in SMJ presented a large improvement in the last 40 years, reaching from 15.5% in 1970 to three times the proportion of forest in 2008. The regeneration of secondary forests in SMJ contradicts the general trend of reduction in tropical forests cover (FAO 2010), but the same process has been observed in other regions of Atlantic Forest (Piotto et al. 2009; Rezende et al. 2015). Added to the fact that the growth of forest cover was a substantial improvement, the increasing of patch size and the aggregation of nearby patches led to the reduction of the number of forest fragments and the overwhelming enhancement of landscape connectivity.

The increase in connectivity can favor the mobility of many species, such as the muriqui, across non-habitat areas, favoring the flow of individuals between populations. Considering that the time-lag in response to extinction could be up to 50 years for primates (Cowlishaw 1999), a mosaic of functionally connected forests could cease the

ongoing extinction process that started with deforestation and impacted the abundance of muriquis. Also, muriquis are able to explore secondary forests (Stallings and Robinson 1991; Pinto et al 1993; Strier 2000), evidencing the importance of forest regeneration in conservation management. Indeed, in the last few years forest regeneration has been recognized as highly relevant for conservation (Chazdon 2008).

Muriquis and where to find them

Habitat patch configuration was notably relevant to predict muriquis occurrence. We found that the area of the smallest forest patch suitable for the muriquis was 170 ha, and although there is no consensus on what is the minimal patch size for this species persistence in the landscape, we obtained results consistent with previous studies (Strier 1987b; Dias and Strier 2003). This is not particularly unpredictable, as muriquis have high energetic requirements due to body size, explore numerous diet components and travel long distances per day (Strier 1987a; Strier 1991). Due to the pattern of deforestation of the Atlantic Forest, in which relief has played a big role, bigger patches usually have more complex shapes (Silva et al. 2007; Freitas et al. 2010), and that could mean habitat heterogeneity and consequently more food availability.

Long-term viable muriqui populations are not often found in the wild (Mendes et al. 2005). For example, the population of muriquis living in the 1,000 ha of the Reserva Particular do Patrimônio Natural Feliciano Miguel Abdala (RPPN-FMA) was estimated as viable for at least the next 100 years (Strier 1996). Also, some large muriqui populations seems viable in large protected areas, such as Serra do Brigadeiro State Park (15,000 ha), Rio Doce State Park (36,970 ha) and Serra do Caparaó National Park (32,000 ha), although more studies are required (PAN Muriquis 2011). In SMJ, despite we found that seven groups of muriquis were distributed in suitable patches, population viability analysis (PVA) for muriqui groups indicates that local extinction could be happening within 30 years in worse case scenarios (Lanna 2015).

Our data suggest that muriquis have reduced capacity in crossing non-habitat areas, as 12 out of 13 groups in SMJ may have been living in the same patch for the last 40 years and only persisted because of forest regrowth. However, long-term field monitoring of populations showed that females are able to cross small amounts of matrix during dispersal events (Tabacow et al. 2009), although routine movements (e.g. foraging) may be much less frequent. Our data confirm that some females risk crossing non-habitat area when dispersing, even if they become solitary (at least three solitary females are found in isolated forest fragments in SMJ).

Out of 1,117 forest fragments in SMJ, only 27 were found to be suitable for muriquis. This could be problematic, because although patch connectivity provides opportunity for colonization of new areas, fragmentation enhances the risk of individuals dispersing from suitable to non-suitable habitat patches (Liao et al. 2013). The fact that some suitable habitat patches showed no occurrence of muriquis indicates that historical factors could be responsible for species absence. We could relate two hypotheses, direct or indirectly, to historical factors: (1) *Those forest fragments were not there in the past*. Since present forest patches are aggregations of several small patches, there was not enough time for species recolonization or demographic expansion to these patches. (2) *There is an ongoing process of extinction of muriquis in SMJ*. The local population could have reached critical values of population density and is unstable and prone to extinction, corroborating PVA analysis (Lanna 2015). The demographic data of muriquis in SMJ shows population growth (Mendes et al. 2005; Lanna 2015), so we

believe that with habitat management that would enlarge forest patches and increase patch connectivity, the effects of fragmentation on the distribution of muriquis (and possibly most of local biodiversity) could be mitigated.

Conclusions

We confirmed and extended a previous report (Santos et al. 2012) of regeneration in forest size since 1970, with a positive balance between deforestation and regeneration. From 1970 to 2008, forest cover increased almost 150%. The number of forest patches was reduced but the size was increased, which reflects the natural regrowth that connected some of the previously isolated patches.

Patch size, connectivity and forest growth were found to influence the distribution of muriquis. Only 27 patches out of the 1,598 patches analyzed in 2008 were identified as suitable in terms of size; 13 provided both sufficient size and potential for flux between groups, although some showed no occurrence of muriquis.

Twelve out of 13 muriqui populations were found in forest remnants that already existed in the 1970s, and they persisted where forest growth rates were higher.

The intense process of deforestation has probably impacted negatively the abundance of muriquis, but their persistence was ensured by forest regeneration and their ability to explore secondary forests, consistent with previous considerations of other muriqui populations (Stallings and Robinson 1991; Pinto et al. 1993; Strier 2000).

This study shows the importance of historical landscape analyses for understanding present distributions and potential for population recovery of endangered species.

References

Aguirre A. 1971. O mono *Brachyteles arachnoides* (E. Geoffroy). Situação atual da espécie no Brasil. Academia Brasileira de Ciências, Rio de Janeiro. 53pp.

Buckland ST, Elston DA. 1993. Empirical models for the spatial distribution of wildlife. Journal of applied Ecology: 478-495.

Burnham KP and Anderson DR. 2004. Multimodel inference understanding AIC and BIC in model selection. Sociological methods & research 33(2): 261-304.

Castellón TD and Sieving KE. 2007. Patch network criteria for dispersal-limited endemic birds of south american temperate rain forest. Ecological Applications 17(8): 2152-2163.

Chazdon RL. 2008. Beyond deforestation: restoring forests and ecosystem services on degraded lands. Science, 320(5882): 1458-1460.

Chiarello AG, De Melo FR. 2001. Primate population densities and sizes in Atlantic forest remnants of northern Espirito Santo, Brazil. International Journal of Primatology 22: 379-396.

CONAMA nº 10, de 1 de outubro de 1993. Estabelece os parametros básicos para análise dos estágios de sucessão de Mata Atlântica. Available: <http://www.mma.gov.br/port/conama/legiabre.cfm?codlegi=135>. Acess: Dec 2016.

Cowlishaw G. 1999. Predicting the pattern of decline of African primate diversity: an extinction debt from historical deforestation. Conservation Biology 13(5): 1183-1193.

Davis A, Wagner JR. 2003. Who knows? On the importance of identifying "experts" when researching local ecological knowledge. Human ecology 31: 463-489.

Dean W. 1997. With broadax and firebrand: the destruction of the Brazilian Atlantic Forest. University of California Press.

Debinski DM, Holt RD. 2000. A survey and overview of habitat fragmentation experiments. Conservation biology 14: 342-355.

Dias LG, Strier KB. 2003. Effects on group size on ranging patterns in *Brachyteles arachnoides hypoxanthus*. Int. J. Primatol. 24: 209-221.

Fahrig L. 2002. Effect of habitat fragmentation on the extinction threshold: a synthesis. Ecological applications 12: 346-353.

Fahrig L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution and Systematics 34: 487–515.

FAO. 2010. Food and Agriculture Organization of the United Nations Global Forest Resources Assessment 2010 FAO Forestry Paper 163.

Fearnside PM. 2008. The roles and movements of actors in the deforestation of Brazilian Amazonia. Ecology and society 13(1).

Ferraz G, Nichols JD, Hines JE, Stouffer PC, Bierregaard RO, Lovejoy TE. 2007. A large-scale deforestation experiment: effects of patch area and isolation on amazon birds. Science 315 (5809): 238–241.

Fischer J and Lindenmayer DB. 2007. Landscape modification and habitat fragmentation: a synthesis. Global Ecology and Biogeography 16(3): 265-280.

Fleishman E, Ray C, Sjögren-Gulve P, Boggs CL and Murphy DD. 2002. Assessing the roles of patch quality, area, and isolation in predicting metapopulation dynamics. Conservation Biology 16(3): 706-716.

Fonseca GAB. 1985. Observation on the ecology of the muriqui (*Brachyteles arachnoides* E. Geofroy 1806): implication for its conservation. Primate Conservation 5: 48-52.

Frankham R. 2007. Efective population size/adult population size ratios in wildlife: a review. Genetical research 89.5-6: 491-503.

Freitas SR, Hawbaker TJ, Metzger, JP. 2010. Effects of roads, topography, and land use on forest cover dynamics in the Brazilian Atlantic Forest. Forest Ecology and Management 259: 410-417.

Groombridge B. (ed.) 1992. Global Biodiversity. Chapman and Hall, London.

Hanski I. 2011. Habitat loss, the dynamics of biodiversity, and a perspective on conservation. AMBIO: A Journal of the Human Environment. 40: 248-255.

Harrel F. 2001. Regression modeling strategies. New York: Spring-Verlag.

Huntington HP. 2000. Using traditional ecological knowledge in science: methods and applications. Ecological applications 10: 1270-1274.

ICMBio. 2016. Brazil Red Book of Threatened Species of Fauna. Brasilia, DF. 75pp.

IEMA. 2007/2008. Ortofotomosaico do Estado do Espírito Santo realizado em 2007/2008. Available: <http://www.meioambiente.es.gov.br>. Acess Jun 2012.

IPEMA. 2007. Espécies da fauna ameaçadas de extinção no Estado do Espírito Santo. (org) Passamani P., Mendes SL. Vitória, ES.

IUCN 2016. IUCN Red List of Threatened Species. <www.iucn.org>. Access: July 2016.

Jenkins CN, Pimm SL and Joppa LN. 2013. Global patterns of terrestrial vertebrate diversity and conservation. Proceedings of the National Academy of Sciences 110(28): E2602-E2610.

Jongman RHG, Ter Braak CFJ, Van Tongeren. 1997. Data Analysis in community and landscape ecology. Cambridge University Press, Cambridge UK.

Lanna AM. 2015. Viabilidade populacional do Muriqui-do-Norte, *Brachyteles hypoxanthus* (Kuhl, 1820) em área fragmentada. Master Thesis.

Laurance WF, Sayer J, and Cassman, KG. 2014. Agricultural expansion and its impacts on tropical nature. Trends in ecology & evolution 29(2), 107-116.

Li Y, Lancaster ML, Cooper SJ, Taylor AC, Carthew SM. 2015. Population structure and gene flow in the endangered southern brown bandicoot (Isoodon obesulus obesulus) across a fragmented landscape. Conservation Genetics 16(2): 331-345.

Liao J., Li Z., Hiebeler DE, Iwasa Y, Bogaert J, Nijs I. 2013. Species persistence in landscapes with spatial variation in habitat quality: a pair approximation model. Journal of theoretical biology 335: 22-30.

Liao J, Ying Z, Hiebeler DE, Wang Y, Takada T and Nijs I. 2015. Species extinction thresholds in the face of spatially correlated periodic disturbance. Scientific reports, 5.

Keesen F, Silva AC, Arashiro E and Pinheiro CFS. 2017. Simulations of populations of Sapajus robustus in a fragmented landscape. Ecological Modelling 344: 38-47.

MacArthur RH, Wilson EO. Theory of Island Biogeography. Princeton University Press, 1967.

Martensen AC, Pimentel RG, Metzger JP. 2008. Relative effects of fragment size and connectivity on bird community in the Atlantic Rain Forest: implications for conservation. Biological Conservation 141(9): 2184-2192.

Mendes SL, Santos RR, Carmo, LR. 2005. Conserving the northern muriqui in Santa Maria de Jetiba, Espirito Santo. Neotrop Primates 13(Suppl):31–35.

Metzger JP. 2000. Tree functional group richness and landscape structure in a brazilian tropical fragmented landscape. Ecological Applications 10: 1147-1161.

Mittermeier RA, Valle CMC, Alves MC, Santos IB, Pinto CAM, Strier KB, Young AL, Veado EM, Constable ID, Paccagnella SG, Lemos de Sá RM. 1987. Current distribution of the muriqui in the Atlantic forest region of Eastern Brazil. Primate Cons. 8:143–149.

Mittermeier RA, Valladares-Pádua C, Rylands AB, Eudey AA, Butynski TM, Ganzhorn, J. U., Kormos, R., Aguiar, J. M., Walker, S. 2006. Primates in peril: The world's 25 most endangered primates, 2004-2006. Primate Conserv 20: 1–28.

Murcia C. 1995. Edge effects in fragmented forests: implications for conservation. Trends in ecology & evolution 10(2): 58-62.

Myers N, Mittermeier RA, Mittermeier CG, Fonseca GAB and Kent J. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853-858.

Pardini R, de Arruda Bueno A, Gardner TA, Prado PI and Metzger JP. 2010. Beyond the fragmentation threshold hypothesis: regime shifts in biodiversity across fragmented landscapes. PLoS One 5(10): e13666.

Pascual-hortal L, Saura S. 2006. Comparison and development of new graph-based landscape connectivity indices: towards the priorization of habitat patches and corridors for conservation. Landscape ecology 21: 959-967.

Pinto LPS, Costa CMR, Strier KB, Fonseca GAB. 1993. Habitat, density and group size of primates in a Brazilian tropical forest. Folia Primatologica 61: 135-143.

Piotto D, Montagnini F, Thomas W et al. 2009. Forest recovery after swidden cultivation across a 40-year chronosequence in the Atlantic forest of southern Bahia, Brazil. Plant Ecol 205:261–272.

Printes RC, Strier KB. 1999. Behavioral correlates of dispersal in female muriquis (*Brachyteles arachnoides*). Int J Primatol 20:941–960.

R Development Core Team. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing; 2016.

Ranta P, Blom TOM, Niemela J, Joensuu E and Siitonen M. 1998. The fragmented Atlantic rain forest of Brazil: size, shape and distribution of forest fragments. Biodiversity & Conservation 7(3), 385-403.

Rezende CL, Uezu A, Scarano FR, Araujo DSD. 2015. Atlantic forest spontaneous regeneration at landscape scale. Biodiversity and Conservation, 24(9): 2255-2272.

Ribeiro MC, Metzger JP, Martensen AC, Ponzoni F, Hirota M.M. 2009. Brazilian Atlantic forest: how much is left and how is the remaining forest distributed? Implications for conservation. Biological Conservation 142: 1141–1153.

Sala OE, et al. 2000. Biodiversity: Global biodiversity scenarios for the year 2100. Science 287(5459): 1770-1774.

Santos AR, Almeida Jr HC and Eugenio FC. 2012. Evolução da cobertura florestal no município de Santa Maria de Jetibá - ES. Floresta e Ambiente 19(3): 296-307.

Saura S, Pascual-hortal L. 2007. A new habitat availability index to integrate connectivity in landscape conservation planning: comparison with existing indices and application to a case study. Landscape and Urban Planning 83: 91-103.

Saura S, Rubio L. 2010 A common currency for the different ways in which patches and links can contribute to habitat availability and connectivity in the landscape. Ecography 33: 523-537.

Sekercioglu CH, Loarie SR, Oviedo Brenes F, Ehrlich PR, Daily GC. 2007. Persistence of forest birds in the Costa Rican agricultural countryside. Conservation Biology 21(2): 482-494.

Silva WG, Metzger JP, Simões S, Simonetti C. 2007. Relief influence on the spatial distribution of the Atlantic Forest cover on the Ibiúna Plateau, SP. Brazilian Journal of Biology, 67(3): 403-411.

Skole D, Tucker C. 1993. Evidence for tropical deforestation, fragmented habitat, and adversely affected habitat in the Brazilian Amazon: 1978–1988. Science 260:1905–1910.

SOS Mata Atlântica/ INPE. 2008. Atlas dos remanescentes florestais da Mata Atlântica: período 2006-2007. Fundação SOS Mata Atlântica.

SOS Mata Atlântica/ INPE. 2014. Atlas dos remanescentes florestais da Mata Atlântica: período 2012-2013. Fundação SOS Mata Atlântica.

SOS Mata Atlântica/INPE. 2015. Atlas dos remanescentes florestais da Mata Atlântica: período 2013–2014. Fundação SOS Mata Atlântica.

Stallings JR, Fonseca GAB, Pinto LPS, Aguiar LMS, Sábato EL. 1991. Mamíferos do Parque Estadual do Rio Doce, Minas Gerais, Brasil. Revista Brasileira de Zoologia 7(4): 663-677.

Strier KB. 1987a. Activity budgets of woolly spider monkeys, or muriquis. American Journal of Primatology 13:385-395.

Strier KB. 1987b. Ranging behavior of woolly spider monkeys. Int. J. Primatol. 8: 575-591.

Strier KB. 1991. Diet in one group of woolly spider monkeys, or muriquis (*Brachyteles arachnoides*). American Journal of Primatology 23:113-126.

Strier, K.B. 1993/1994. Viability analyses of an isolated population of muriqui monkeys (*Brachyteles arachnoides*): implications for primate conservation and demography. Primate Conservation 14-15: 43-52.

Strier KB. 2000. Population viability and regional conservation priorities for muriquis (*Brachyteles arachnoide*s) in Brazil's Atlantic forest. Biotropica 32(4b): 903-913.

Tabacow FP, Possamai CB, de Melo FR, Mendes SL, Strier KB. 2009. New sightings of northern muriqui (*Brachyteles hypoxanthus*) females in forest fragments surrounding the Estação Biológica de Caratinga-RPPN Feliciano Miguel Abdala, Minas Gerais, Brasil. Neotrop Primates 16:67–69.

Taberelli M, Gascon C. 2005. Lessons from fragmentation research: improving management and policy guidelines for biodiversity conservation. Conservation Biology 19: 734 – 739.

Taylor PD, Fahrig L, Henein K, Merriam G. 1993. Connectivity is a vital element of landscape structure. Oikos, 571-573.

Uezu A, Beyer DD and Metzger JP. 2008. Can agroforest woodlots work as stepping stones for birds in the Atlantic forest region?. Biodiversity and Conservation 17(8): 1907-1922.

Watts K, Vanhala T, Connolly T, Cottrell J. 2016. Striking the right balance between site and landscape-scale conservation actions for a woodland insect within a highly fragmented landscape: A landscape genetics perspective. Biological Conservation, 195: 146-155.

Wilcove DS, McLellan CH and Andrew PD. 1986. Habitat fragmentation in the temperate zone. Conservation biology 6: 237-256.

Capítulo 2

Percepções sobre como a fragmentação do habitat afeta a dispersão e o movimento de uma espécie de primata macho-filopátrica

---

Insights on how habitat fragmentation affects dispersal and movement of a male-philopatric primate species

Introduction

Movements of individuals, whether for dispersal or routine, represent an important aspect of an organism's life history (Bowman et al. 2002). They can vary from small-scale movements, e.g. foraging within a habitat patch, to migratory events on a regional scale (Ims 1995). Currently, in a world of highly fragmented natural landscapes, it is convenient to identify different types of movement behavior and how they contribute to the understanding of dispersal processes (Fahrig 2003). Bender et al. (2003) and Tischendorf et al. (2003) found that the amount of habitat around a patch is strongly related to animal movement among patches. All individuals engage in routine movements, but dispersal movements may vary among populations and among individuals (Bowler and Benton 2005).

Species that move between habitat patches in fragmented landscapes face great risks. Even though dispersal mortality varies among different landscapes, it is highly relevant to identify factors that lead to the disruption of movement (Mennechez et al. 2003). Dispersing individuals may face threats related to predation, starvation or even unfamiliarity of habitat. In a fragmented habitat, in which population densities can be very low, they can also face low reproductive success as mating opportunities are reduced (Bengtsson 1978).

Dispersal processes play an important role in population regulation, genetic structure and spatial distribution (Dunning et al. 1995; Ibrahim et al. 1996; Hanski and Gilpin 1997; Sutherland et al. 2000; Clobert et al. 2001; Bowler and Benton 2005). Some of the evolutionary reasons for animals to disperse include inbreeding avoidance (e.g. Pusey 1987; Clutton-Brock 1989; Wolff 1994), mate choice (Dobson 1982) and resource competition (Greenwood 1980). The avoidance of resource competition may also explain the shift from cohesive to fluid, fission–fusion grouping patterns (Chapman et al. 1995; Aureli et al. 2008).

In most mammals, dispersal is prevalent in one sex, while the other stays in their natal groups (Greenwood 1980). In primates, female dispersal is widespread among some taxa, including colobids (e.g. Qi et al. 2009), apes (e.g. Nishida et al. 2003) and atelids (e.g. Strier 1994). Females habitually disperse during puberty in species in which the average span of male residence in a group commonly exceeds the age of females at first breeding (Pusey and Packer 1987; Lukas and Clutton-Brock 2011). Thus, female dispersal occurs before sexual interactions initiate, avoiding mating with close kin males.

Among primates with female-biased dispersal patterns, the northern muriqui, *Brachyteles hypoxanthus* (Atelidae) is a diurnal and arboreal species, with nonhierarchical, egalitarian relationships among males and females (Strier et al. 2015), similar to other atelins (Strier 2005; 2014; Strier and Mendes 2009, 2012). Males are philopatric and females typically migrate from their natal group when they reach puberty (Printes and Strier 1999; Strier and Ziegler 2000; Strier et al. 2015). They often become solitary when they reach adulthood due to the lack of other social groups in fragmented habitats (Mendes et al. 2005).

The northern muriqui is a “critically endangered species” (IUCN 2013; ICMBio 2016; IPEMA 2007), endemic to the Atlantic Forest in Brazil. Its historical distribution used to encompass montane forests of Bahia, Espírito Santo and Minas Gerais states (Aguirre 1971). In Espírito Santo (ES), the historical and current records of muriquis are restricted to the southern montane forests. Nevertheless, due to forest fragmentation and

destruction, the populations of muriquis are extinct or at low densities in much of their historical range (Aguirre 1971; Mittermeier et al. 1987).

Here we present a set of empirical field observations on muriqui female dispersal in isolated groups and group movements among different forest fragments over a 15 years period. We also provide insights on how forest fragmentation could affect dispersal and movement patterns and its implications for habitat management and conservation strategies for this species.

Santa Maria de Jetibá and groups of muriquis

In Santa Maria de Jetibá (SMJ), groups of muriquis can be found in at least 13 small isolated forest fragments (Mendes et al. 2005), surrounded mainly by agricultural crops in a mosaic of small private properties. Five out of 13 groups of muriquis ((MB) Mata do Belém, (RP1 and RP2) Rio das Pedras 1 and 2, (CO1 and CO2) Córrego do Ouro 1 and 2) have been continuously monitored since 2002 as part of a plan to improve the prospects of local conservation of this species (Figure 2.1).

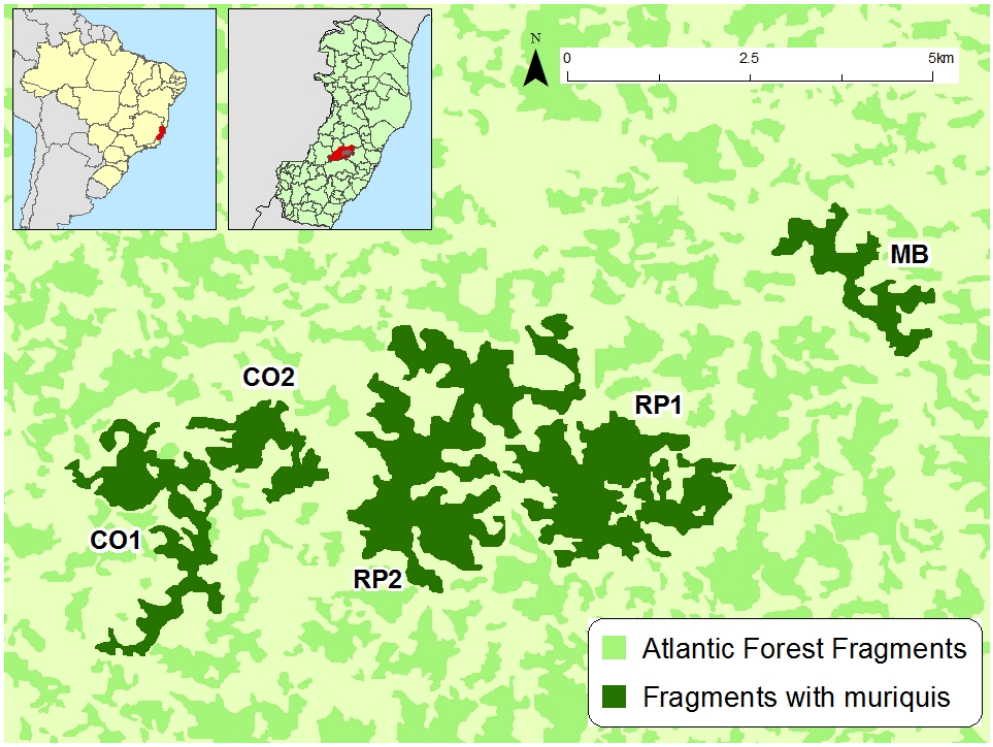


Figure 2.1. Five monitored groups of muriquis in Santa Maria de Jetibá, ES, Brazil ((MB) Mata do Belém, (RP1 and RP2) Rio das Pedras 1 and 2, (CO1 and CO2) Córrego do Ouro 1 and 2.

Although the Atlantic Forest in the region was intensively fragmented in the past, reaching less than 15% of native forest, forest regrowth attained almost 150% during the last four decades (Santos et al. 2012; confirmed and extended with data in chapter 1). The annual census of the five monitored groups of muriquis (which represent more than 80% of the known population in the central-southern region of ES) also shows

population growth: from 52 individuals in 2004 (Mendes et al. 2005) to 91 in 2016. The intense process of deforestation in SMJ has probably impacted negatively the abundance of muriquis, but their persistence and regrowth was ensured by forest regeneration and their ability to explore secondary forests, consistent with previous observations of other muriqui populations (Pinto et al. 1993; Strier 2000). Other factors contribute to muriqui population maintenance: local human populations present a family agrarian structure and the tradition of poaching primates is not usual at present time.

The Muriqui Project – ES and data collection for 15 years

The Muriqui Project – ES is a long-term study that has been systematically monitoring groups of muriquis in SMJ since 2002. Since 2014, the State Action Plan for Muriqui Conservation was officially recognized by the State Government under Regulation nº 02/2014 and is currently coordinated by the State Secretary of Environment.

As these groups have been continuously observed over the last 15 years, we were able to collect many ecology and behavior data about muriquis, together with information on population demography and distribution, including life history data of females and empirical data on the movements of muriquis from five different groups.

Life history data of females. Female ages at dispersion and first reproduction were determined via annual census observations. The ages of young females (infants, juveniles and subadults) born before 2002 were estimated by comparing their characteristics with those of females of known age. Also, as part of an ongoing management program of this project, two 6-year old females were translocated (captured and released) to other groups of muriquis. The first one was successfully translocated in 2005 (Mendes et al. 2005) from an isolated group (MB) to another isolated group (CO1); the second was released in Augusto Ruschi Biological Reserve (a 3,573 ha protected forest 20 km away) in 2016 and is currently being monitored via radio-telemetry.

Empirical data on the movement of muriquis. We were also able to observe and register rare but significant movement events. Thus, our information on the movements of groups of muriquis between fragments in SMJ was obtained *Ad Libitum*, i.e., we recorded the events we thought to be relevant to our research with no systematic constraints, at the very moment and place in which we observed them.

Female dispersal

Between 2002 and 2015, we counted 49 female individuals in five different groups of muriquis. At least 30 females were born and at least 21 reached puberty during this period (recall that females that reached puberty could have been born prior to 2002). One adult female and three infants were presumed dead because their ages, when they disappeared, were not close to dispersal age (following criteria of Strier et al. 2006 and Strier et al. 2015). The current distribution of females in the five groups studied is summarized in Table 2.1. Of the 21 females, at least six emigrated (or died) prior to first parturition but this number could be up to 14 (Table 2.2). Yet, at least five females (three from MB, one from RP1 and one from RP2) stayed in their natal group and became sexually active and reproducing.

Even though we could not exclude the possibility that females died before dispersing, mortality rates of subadult muriquis in SMJ are very low (Lanna 2015). So, it is more likely that these females could have emigrated to one of the monitored groups, to a yet to be discovered group or are solitary in a nearby forest fragment. And as we did not know females individually, we could not determine the potential natal groups of females that immigrated into monitored groups. They could have originated from one of the studied groups or from another group in the region that had not yet been discovered.

We have no records of a female returning to her natal group after becoming sexually active and reproducing, a fact consistent with what has been observed by Strier et al. (2015) in Reserva Particular do Patrimônio Natural Feliciano Miguel Abdala (RPPN-FMA), according to whom there seems to be no secondary dispersal after the onset of puberty and sexual activity.

Table 2.1. Females of muriquis in five groups in Santa Maria de Jetibá, ES, Brazil. (MB) Mata do Belém, (RP1 and RP2) Rio das Pedras 1 and 2, (CO1 and CO2) Córrego do Ouro 1 and 2.

Age Classes	MB	RP1	PR2	CO1	CO2
Infant	3	2	3	2	2
Juvenile	2	3	2	0	0
Subadult	0	1	1	0	2
Adult	6	5	6	6	3
Total of females	11	11	12	8	7

Table 2.2. Summary of possible events of emigration and immigration of females of muriquis in five groups in Santa Maria de Jetibá, ES, Brazil. (MB) Mata do Belém, (RP1 and RP2) Rio das Pedras 1 and 2, (CO1 and CO2) Córrego do Ouro 1 and 2.

Social group	Total of females	Emigration	Immigration	Known emigration	Other possible emigrations	Known immigration	Other possible immigrations
MP	6	2-3	0	2	1	0	0
RP1	4	0-2	1-3	0	1 or 2	1	1 or 2
RP2	5	0-5	2-5	1	1,2, 3 or 4	2	1,2, or 3
CO1	4	0-4	1	3	1	2***	0
CO2	?	?	2	?	?	2	?
		2-14	5 - 11	6	$\geq$ 4 more, up to 8 possible	7	2-5 more possible

** Total of females with minimal dispersal age (following criteria of age in Strier, et al. 2006; born before 2009). ** Includes translocated female. If excluded, two emigrations considering 5 females. *** Inlcudes translocated female. If excluded, one confirmed immigration.*

In MB, two females left their group and did not find any other group to migrate, remaining within the same forest fragment. Mendes et al. 2005 recorded another two solitary females (and possibly three others) in SMJ, of unknown origin. Even in relatively large populations with more than one social group in a forest fragment, such as RPPN-FMA, Tabacow et al. (2009) sighted four solitary females located in the surrounding forests and recognized that at least three of them were originated from the groups studied in the RPPN-FMA.

In a source-sink dynamics (Pulliam 1988), these forest fragments with solitary females could be represented as "sink", due to the absence of mating opportunities with adult males. However, fragments like these may be beneficial in supporting ongoing efforts to increase the available habitat for muriquis by establishing protected corridors (Strier et al. 2015).

The isolation of the MB group also led to high inbreeding rates. Genetic variability inside the group is low enough as to make it impossible to determine the paternity of some individuals (Chaves et. al. in prep/ pers. comm.). High inbreeding rates within social groups caused by habitat isolation have also been recorded for other primate species. Clarke et al. (2002) and Gonçalves et al. (2003) found that howler monkeys and marmosets, respectively, when inhabiting isolated forest fragments, changed foraging and activity patterns, social organization and physiological conditions, which also led to incestuous sexual relationships.

The project in SMJ focused initially on conducting census of muriqui groups in order to increase the knowledge about this population and systematically monitor the behavior of individuals of the MB group; over the years, monitoring was extended to other groups. Since 2012, we increased our efforts to identify muriquis individually by their natural facial markings and fur in all five groups (not only MB). So, even though we currently have individualized data only for females pertaining to the MB group, for future studies we will have life history data of individualized females born in the MB group since 2002 and of all females born in the other four groups since 2012.

Renata, the translocated female. In 2005, a 6-year old female was successfully captured from her natal group in MB and relocated to CO1 (10 km away), close to the muriqui group. Her age was within the known average dispersal age for females of muriquis. At first, Renata needed the protection of adult males from the harassment of adult females in CO1, similarly to what has been previously described for new female immigrants in the RPPN-FMA population (Strier 1999). However, within two weeks, she was already following the group and interacting peacefully with both males and females. She had her first parturition three years later (Oct 2008), but the infant was presumed dead after disappearing one year after birth. In Aug 2010 she had her second parturition, Régia (a female infant), and she gave birth to other two infants after that (one female at the end of 2013 and one male at the end of 2015). At the beginning of 2016, 6-year old Régia disappeared; we believe that this was most probably due to migration, as her age was close to dispersal age.

Colonization of a new forest fragment

Back in the 1970's, CO1 and CO2 consisted in a single social group with approximately 20 individuals (at least nine adults, seven males and two females), probably living in a 20 ha forest fragment. Over the last 40 years, the restoration of forests aggregated this remnant to other adjacent ones, resulting in a 210 ha habitat. In 2005, two males, one adult and one subadult, disappeared for months before they were sighted again, probably exploring areas outside the group's home range. They finally disappeared with other six individuals (at least 2 adult females) in 2006 and were found only two years later, living in a surrounding forest fragment of 75 ha.

In 2006, it was established that the original CO group fissioned into two different social groups. The group living in the original forest patch, presently called CO1, increased to 18 individuals and expanded its home range; the smaller group (with the same eight individuals), now named CO2, migrated to another fragment across the road and an eucalyptus plantation (Figure 2.2). Currently, CO1 has 23 individuals and CO2 has 14 (last census conducted from Nov 2015 to Jun 2016). This has been the only reported event of movement across different forest patches (other than the expected female dispersal) during the 14 years of muriqui population monitoring in SMJ.

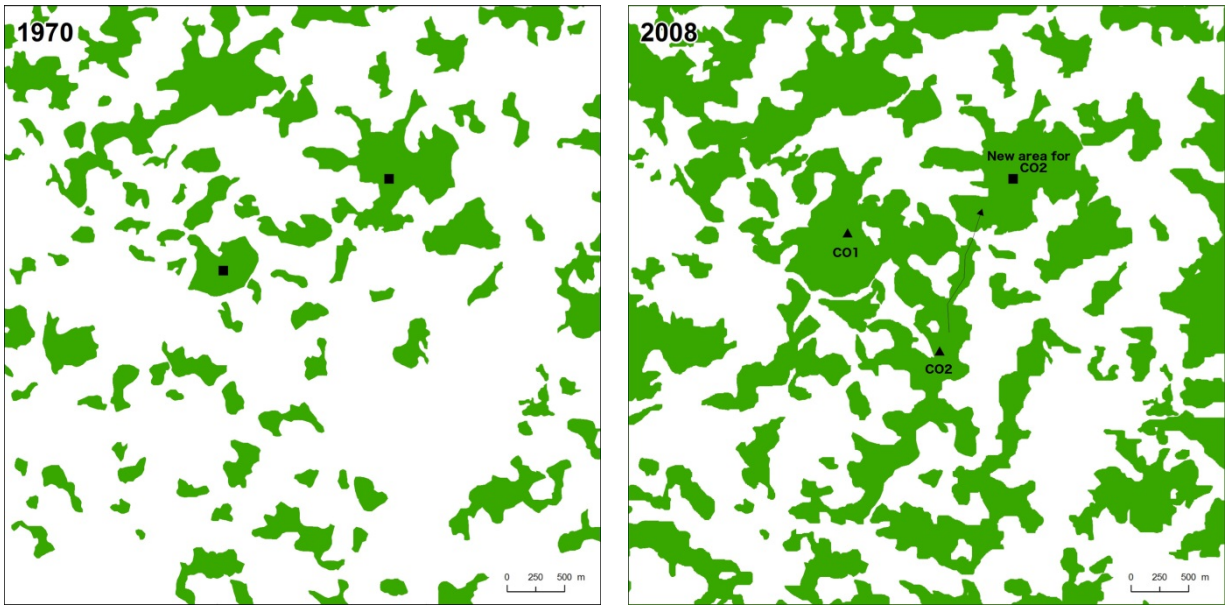


Figure 2.2. Past and current distribution of a group of muriquis before and after fission in Santa Maria de Jetibá, ES, Brazil. Map A shows landscape in 1970 and two possible areas of past occurrence of the CO group (black squares). Map B shows the landscape in 2008, together with the locations of groups CO1 and CO2 after fission (black triangles), a possible movement route (black arrow) and the new location of group CO2 (black square).

We feel that this event of colonization is somehow unexpected, as the migration of a group to a new forest habitat through a non-habitat matrix has not been previously documented for muriquis in a fragmented landscape. However, the observation that young sexually mature males were the ones that explored new territory and established the new group is consistent with previous reports for muriquis (Strier et al. 1993; Dias and Strier 2003). Other atelids are observed only occasionally to leave the trees and

walk along the ground (Glander, 1992; Mandujano et al. 2004). Mandujano et al. 2004 also suggested that howler monkeys movement among forest fragments is not random; spatial configuration of habitat patches and the nature of the surrounding matrix may be critical in determining movement patterns.

Habitat fragmentation vs. movement and dispersal

Even though we do not have sufficient data to perform complex statistical analyses, the field data collected over the years in SMJ provided some insights on how habitat fragmentation alters muriquis patterns of movement and dispersal across landscapes. We mapped forest fragments from 1970 and 2008, quantified forest connectivity using graph theory (for more information, see chapter 1) and we know where the groups of muriquis are currently distributed. In addition, as most of the knowledge about the biology of muriquis – obtained from a long-term field research at RPPN-FMA, a privately owned protected forest in Caratinga, Minas Gerais (Strier 2014; Strier and Mendes 2012) – is well established, it was also possible to identify changes in typical movement behavior.

The summary of events of female dispersal and group movement along with habitat connectivity data provided a baseline to the development of a conceptual map to predict movement behavior of muriquis across fragmented landscapes (Figure 2.3).

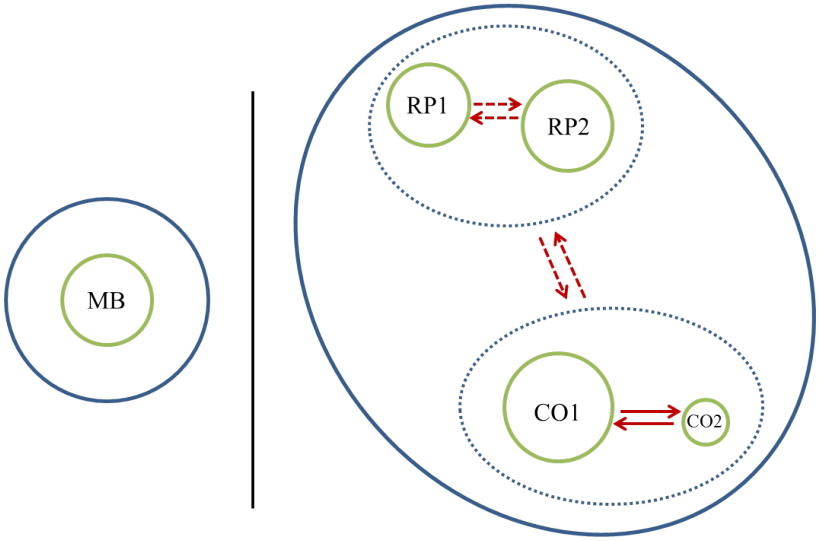


Figure 2.3. Conceptual map of how habitat fragmentation could affect group movement and female dispersal of muriquis across landscapes with different forest connectivity. Five muriqui groups are indicated by green circles with diameters proportional to the number of females in the group ((MB) Mata do Belém, (RP1 and RP2) Rio das Pedras 1 and 2, (CO1 and CO2) Córrego do Ouro 1 and 2). Blue circles indicate the components to which forest fragments belong; dashed blue circles indicate subcomponents. Isolated forest patches (barrier shown in black line) result in a complete change of typical behavior of muriquis while forest patches functionally connected maintain typical behavior. Movement among connected (red arrows) and partially connected (dashed red arrows) forest patches may occur if they belong to the same component (note: in graph theory, a component encompasses different patches that are connected and a subcomponent encompasses groups of patches that are connected by a path).

Our landscape data show that MB is an isolated forest patch, poorly connected to other patches and surrounded by a road and a river reservoir. Out of six females at dispersal age, three stayed in their natal group, two migrated to the same forest patch and became solitary and one was translocated to CO1. Also, no immigration events to MB were recorded.

In the RP complex, in which fragments are partially connected to each other, some females stayed in their natal group (at least two, but probably more), also showing changes from expected behavior. Still, events of emigration and immigration were recorded. Even though no records of movement among patches were observed, connectivity between them could potentially allow it to occur eventually.

In the CO complex, in which patches have the higher connectivity indexes in the landscape, typical behavior of female dispersal was ensured. None of the females stayed in their natal group and we recorded immigration events. Also, we observed a single group movement from one forest patch to another.

Implications for Conservation

An important challenge in managing wildlife populations is to understand patterns of habitat changes through time. As presented above, patch connectivity and isolation between muriqui groups are key factors for ensuring population viability. Thus, we can recognize the importance of three recommended conservation strategies which can be implemented in SMJ region: 1) improving connectivity between patches, 2) establishing a protected corridor of biodiversity, and 3) translocation of young females to other groups within SMJ landscape.

SMJ landscape has today much larger patches than it had in the past. This means that the lack of habitat is not a problem for the maintenance of a muriqui population in the region. The real problem is that there are few remnants of muriqui groups confined to few forest fragments. So, the first conservation strategy, *improving connectivity between patches*, can maintain connectivity among populations, allow the colonization of empty fragments and expand population home range. Since maintaining connectivity among populations is considered to be an essential part of modern conservation (Chetkiewicz et al. 2006; Killeen et al. 2014), this represents a great advantage in terms of supporting ongoing efforts to increase the available habitat for muriquis.

The most widely used approach for maintaining connectivity is *establishing a protected corridor of biodiversity*, a region of landscape that facilitates the movement of organisms between populations and is protected through some kind of government regulation (Zeller et al. 2012; Vasudev 2015). One approach has been to map costs of species movement though heterogeneous matrix among habitat patches (for more information on simulation of movements of muriquis, see chapter 3) to characterize how landscape variables affect animal movement. Thus, predicting the effects of landscape modifications allows us to prioritize which habitats to protect and to inform management decisions relating to corridors.

Since the dispersal rate of females of muriquis is probably lower than the deforestation rate in SMJ, especially due to the isolation of forest patches, the *translocation of young females to other groups within SMJ landscape* will certainly provide better conditions

for persistence of species in a regional scale. There have been made a few successful attempts of neotropical primates translocation, in order to improve genetic flux and diversity among groups. Its use as a conservation tool for primates has been limited to rescue operations in flooded forests (Konstant and Mittermeier 1982; Richard-Hansen et al. 2000; Marques et al. 2011). Indeed, even though only three young females of muriquis have been translocated so far, translocation has proved to be an efficient alternative procedure for species management. Besides Renata, another young female was translocated within the state of Minas Gerais, from an isolated forest to privately owned area RPPN Recanto do Sossego and has already had two parturitions (PAN Muriqui 2011).

Our data suggest that the combination of population demography information and landscape data on habitat fragmentation can extend our plan to improve conservation and management of muriquis and restoration of Atlantic Forest. The extrapolation from the consistent patterns found in female dispersal age over time in RPPN-FMA (Strier and Mendes 2012, Strier et al. 2015) and across groups in SMJ (this study) can help insure that there will be females of this species to disperse in the future (for more information, see chapter 3). We could predict muriqui behavior not only for our study population but also for muriquis living elsewhere under different conditions. Our efforts in reducing the risk of extinction of muriquis include not only translocation of females as a population management strategy, but also improving the connectivity between forest fragments.

References

Aguirre A. 1971. O mono *Brachyteles arachnoides* (E. Geoffroy). Situação atual da espécie no Brasil. Academia Brasileira de Ciências, Rio de Janeiro. 53pp.

Aureli F, Schaffner CM, Boesch C, Bearder SK, Call J, Chapman CA, Connor R, Di Fiore A, Dumber RIM, Henzi SP, Holekamp K, Korstjens AH, Layton R, Lee P, Lehmann J, Manson JH, Ramos-Fernandez G, Strier KB, van Schaik CP. 2008. Fission-fusion dynamics: new research frameworks. Curr Anthropol 49:627–654.

Bender D., Tischendorf L., Fahrig L. 2003. Using patch isolation metrics to predict animal movement in binary landscapes. Landscape Ecology 18: 17–39.

Bengtsson BO. 1978. Avoiding inbreeding: at what cost? J. theor. Biol. 73: 439–444.

Bowler DE, Benton TG. 2005 Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biological Review 80, 205–225.

Bowman J, Jaeger JAG, Fahrig L. Dispersal distance of mammals is proportional to home range size. 2002. Ecology 83(7): 2049–2055.

Chapman CA, Chapman LJ, Wrangham RW. 1995. Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. Behav Ecol Sociobiol 36:59–70.

Chetkiewicz CLB, Clair CCS, Boyce MS. 2006 Corridors for conservation: integrating pattern and process. Ann Rev Ecol Evol Syst. 37: 317-342.

Clarke MR, Collins DA, Zucker EL. 2002. Responses to deforestation in a group of mantled howlers (*Alouatta palliata*) in Costa Rica. Int. J. Primatol 23:365–381.

Clobert J, Danchin E, Dhondt AA, Nichols JD. 2001. Dispersal. Oxford University Press: New York.

Clutton-Brock TH. 1989. Female transfer and inbreeding avoidance in social mammals. Nature 337:70–72.

Dias LG, Strier KB. 2003. Effects of group size on ranging patterns in *Brachyteles arachnoides hypoxanthus.* International Journal of Primatology 24(2): 209-221.

Dobson FS. 1982. Competition for mates and predominant juvenile male dispersal in mammals. Anim Behav 30:1183–1192.

Dunning JBJ, Stewart DJ, Danielson BJ, Noon BR, Root TL, Lamberson R.H., Stevens E.E. 1995. Spatially explicit population models: current forms and future uses. Ecological Applications 5: 3–11.

Fahrig L. Effects of habitat fragmentation on biodiversity. 2003. Annual Review of Ecology, Evolution and Systematics 34:. 487–515.

Glander, KE 1992. Dispersal patterns in Costa Rica mantled howling monkeys. Int. J. Primatol 13:415–436.

Gonçalves EC, Ferrari SF, Silva A, Coutinho PEG, Menezes EV, Schneider MPC. 2003. Effects of habitat fragmentation on the genetic variability of silvery marmosets, *Mico argentatus*. In Primates in Fragments: Ecology and Conservation. Marsh, LK, (ed.), pp. 17–28. Kluwer Academic/ Plenum Publishers. New York.

Greenwood P. 1980. Mating systems, philopatry and dispersal in birds and mammals. Anim Behav 28:1140–1162.

Hanski I, Gilpin ME. 1997. Metapopulation biology: ecology, genetics and evolution. Academic Press: San Diego.

Ibrahim KM, Nichols RA, Hewitt GM. 1996. Spatial patterns of genetic variation generated by different forms of dispersal during range expansion. Heredity 77: 282-291.

ICMBio. 2016. Brazil Red Book of Threatened Species of Fauna. Brasilia, DF. 75pp.

Ims R.A. Movement patterns related to spatial structures. 1995. (Eds) Hansson L., Fahrig L., Merrian G. In: Mosaic landscapes and ecological processes, Chapman, London. pp 85–109.

IPEMA. 2007. Espécies da fauna ameaçadas de extinção no Estado do Espírito Santo. (org) Passamani P., Mendes SL. Vitória, ES.

IUCN 2016. IUCN Red List of Threatened Species. <www.iucn.org>. Access: July 2016.

Killeen J, Thurfjell H, Ciuti S, Paton D, Musiani M, Mark S Boyce. 2014. Habitat selection during ungulate dispersal and exploratory movement at broad and fine scale with implications for conservation management. Mov Ecol. 2:15.

Konstant WR, Mittermeier, RA. 1982, Introduction, reintroduction and translocation of Neotropical primates: past experiences and future possibilities. International Zoo Yearbook, 22: 69–77.

Lukas D, Clutton-Brock TH. 2011. Group structure, kinship, inbreeding risk and habitual female dispersal in plural-breeding mammals. J Evol Biol 24:2624–2630.

Mandujano S, Escobedo-Morales LA, Palacios-Silva R. Movements of *Alouatta palliata* Among Forest Fragments in Los Tuxtlas, Mexico. 2004. Neotropical Primates 12(3): 126-131.

Marques AAB, Schneider M, Alho, CJR. 2011. Translocation and radiotelemetry monitoring of black-tailed marmosets, *Callithrix* (Mico) melanura (É. Geoffroy in Humboldt), in a wildlife rescue operation in Brazil. Brazilian Journal of Biology 71(4): 983-989

Mendes SL, Santos RR, Carmo, LR. 2005. Conserving the northern muriqui in Santa Maria de Jetiba, Espirito Santo. Neotrop Primates 13(Suppl):31–35.

Mennechez G., Schtickzelle N., Baguette M. 2003. Metapopulation dynamics of the bog fritillary butterfly: Comparison of demographic parameters and dispersal between continuous and a highly fragmented landscape. Landscape Ecology 18: 279–291.

Mittermeier RA, Valle CMC, Alves MC, Santos IB, Pinto CAM, Strier KB, Young AL, Veado EM, Constable ID, Paccagnella SG, Lemos de Sá RM. 1987. Current distribution of the muriqui in the Atlantic forest region of Eastern Brazil. Primate Cons. 8:143–149.

Nishida T, Corp N, Hamai M, Hasegawa T, Hiraiwa-Hasegawa M, Hosaka K, Hunt KD, Itoh N, Kawanaka K, Matsumoto-Oda A, Mitani JC, Nakamura M, Norikoshi K, Sakamaki T, Turner L, Uehara S, Zamma K. 2003. Demography, female life history, and reproductive profiles among the chimpanzees of Mahale. Am J Primatol 59:99–121.

Pinto LPS, Costa CMR, Strier KB, Fonseca GAB. 1993. Habitat, density and group size of primates in a Brazilian tropical forest. Folia Primatologica 61: 135-143.

Printes RC, Strier KB. 1999. Behavioral correlates of dispersal in female muriquis (*Brachyteles arachnoides*). Int J Primatol 20:941–960.

Pusey AE. 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. Trends Ecol Evol 2:295–299.

Pusey AE, Packer C. 1987. Dispersal and philopatry. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 250–266.

Qi XG, Li BG, Garber PA, Ji W, Watanabe K. 2009. Social dynamics of the golden snubnosed monkey (*Rhinopithecus roxellana*): female transfer and one-male unit succession. Am J Primatol 71:670–679.

Richard-Hansen C, Vié JC, Thoisy B. 2000. Translocation of red howler monkeys (*Alouatta seniculus*) in French Guiana. Biological Conservation 93(2): 247-253.

Santos AR, Almeida Jr HC and Eugenio FC. 2012. Evolução da cobertura florestal no município de Santa Maria de Jetibá - ES. Floresta e Ambiente 19(3): 296-307.

Stallings JR, Fonseca GAB, Pinto LPS, Aguiar LMS, Sábato EL. 1991. Mamíferos do Parque Estadual do Rio Doce, Minas Gerais, Brasil. Revista Brasileira de Zoologia 7(4): 663-677.

Strier KB. 1994. Myth of the typical primate. Am J Phys Anthropol 37(S19):233–271.

Strier KB. 1999. Why is female kin bonding so rare? Comparative sociality of New World primates. In Lee, P. C. (ed): Comparative Primate Socioecology, Cambridge University Press, Cambridge, pp. 300-319.

Strier KB. 2000. Population viability and regional conservation priorities for muriquis (*Brachyteles arachnoide*s) in Brazil's Atlantic forest. Biotropica 32(4b): 903-913.

Strier KB. 2005. Reproductive biology and conservation of muriquis. Neotrop Primates 13(Suppl):41–47.

Strier KB. 2014. Northern muriqui monkeys: behavior, demography, and conservation. In: Yamagiwa J, Karczmarski L (eds) Primates and cetaceans: field studies and conservation of complex mammalian societies. Springer, New York, pp 233–247.

Strier KB, Mendes SL. 2009. Long-term field studies of South American Primates. In: Garber PA, Estrada A, Bicca-Marques JC, Heymann EW, Strier KB (eds) South American primates: comparative perspectives in the study of behavior, ecology, and conservation. Springer, New York, pp 129–155.

Strier KB, Mendes SL. 2012. The northern muriqui (*Brachyteles hypoxanthus*): lessons on behavioral plasticity and population dynamics from a critically endangered primate. In: Kappeler P, Watts D (eds) Long-term studies of primates. Springer, Heidelberg, pp 125–140

Strier KB, Ziegler TE. 2000. Lack of pubertal influences on female dispersal in muriqui monkeys, *Brachyteles arachnoides*. Anim Behav 59(4):849–860.

Strier KB, Mendes FD, Rímoli J, Rímoli AO. 1993. Demography and social structure of one group of muriquis *(Brachyteles arachnoides*). International Journal of Primatology 14(4): 513-526.

Strier KB, Boubli JP, Possamai CB, Mendes SL. 2006. Population demography of northern muriquis (*Brachyteles hypoxanthus*) at the Estação Biológica de Caratinga/Reserva Particular do Patrimônio Natural-Feliciano Miguel Abdala, Minas Gerais, Brazil. Am J Phys Anthropol 130(2):227–237.

Strier KB, Possamai, CB, Mendes SL. 2015. Dispersal Patterns of Female Northern Muriquis: Implications for Social Dynamics, Life History, and Conservation. (Eds) Takeshi F., Yamagiwa J, Aureli

F. In: Dispersing Primate Females: Life History and Social Strategies in Male-Philopatric Species. Primatology Monographs. pp 3-22.

Sutherland, G.D., Harestad A.S., Price K., Lertzman K.P. 2000. Scaling of natal dispersal distances in terrestrial birds and mammals. Conservation Ecology 4(1):16. [online]

Tischendorf L, Bender DJ, Fahrig L. 2003. Evaluation of patch isolation metrics in mosaic landscapes for specialist vs. generalist dispersers. Landscape Ecology 18:41–50.

Wolff J.O. 1994. More on juvenile dispersal in mammals. Oikos 71: 349–352.

Zeller KA, McGarigal K, Whiteley AR. 2012. Estimating landscape resistance to movement: a review. Landsc Ecol. 27:777–797.

Capítulo 3

Simulação da dinâmica espacial de populações de muriquis em paisagens fragmentadas

---

Simulating spatial dynamics of muriqui populations within fragmented landscapes

Introduction

Habitat connectivity constitutes a crucial factor for the persistence of species in a landscape, with critical consequences for the dynamics of populations. In heterogeneous fragmented landscapes, the linkages between habitat patches can enhance species persistence through multiple mechanisms (Lindenmayer et al. 2008; Doerr et al. 2011), including colonization of new areas (Thomas 1994; Hanski 1998), recolonization of unoccupied habitat (Fahrig and Merriam 1994; Moilanen and Hanski 2001) and inbreeding avoidance (Bengtsson 1978; Swart and Lawes 1996). Even though patch connectivity provides opportunity for species to spread through the landscape, fragmentation increases the risk of individuals to disperse from suitable to non-suitable habitat patches (Liao et al. 2013). This is particularly true for species with high energetic requirements and reduced capacity to cross non-habitat areas (Fleishman et al. 2002; Uezu et al. 2005).

The northern muriqui, *Brachyteles hypoxanthus*, is a critically endangered primate (IUCN 2013; ICMBio 2016; IPEMA 2007) endemic to the Atlantic Forest in Brazil, with its remaining population threatened primarily by habitat loss and fragmentation (Mittermeier et al. 1987; Mendes et al. 2005a). Effective muriqui management and conservation planning require a good understanding of population dynamics (ICMBio 2011). Habitat size and connectivity, essential characteristics for many wildlife species (e.g. birds (Martensen et al. 2008); mammals (Gehring and Swihart 2003); amphibians (Cushman 2006)), play a crucial role in the population dynamics of muriquis (confirmed with data in chapter 1). As already demonstrated for muriqui populations, habitat features influence social organization, foraging, mating, dispersal events, demography and the spatial distribution of individual animals (Pinto et al. 1993; Strier 2000; Dias and Strier 2003; Mendes et al. 2005b).

Integrating life history of muriquis with landscape data in computer models provide us with tools to evaluate future impacts of various threats. However, previous models of muriqui population dynamics, while making important contributions, have not incorporated spatially explicit data or events. For instance, models for the analysis of population viability have been developed for a single population (Strier 1993/1994) as well as for all muriqui populations (Rylands et al. 1998; Brito and Grelle 2006; Brito et al. 2008; Eduardo and Brito 2012; Lanna 2015). However, such models did not take into account the dynamic dispersal of individuals in a heterogeneous landscape. Santos (2013), using a cellular automata model, simulated the dispersal of muriquis in a fragmented landscape but did not incorporate a population dynamics model with age classes or annual time steps.

To help fill these information gaps, we developed and implemented an individual-based, spatially-explicit model that incorporates population dynamics of muriquis and thus is a suitable base for evaluating, through simulations, the importance of landscape features on muriqui movement and population growth. We simulated how the spatial configuration of suitable habitat patches affects population spread and growth through a heterogeneous matrix in a fragmented landscape. By combining the approaches of different models – a spatially explicit model with a population dynamics model – we could understand possible population responses to landscape variables in a time lapse (e.g. Söndgerath and Schröder 2002; BenDor et al. 2009; Carter et al. 2015; Keesen et al. 2017).

Agent-based models

Individual-based models (also referred as ABM, agent-based models) are a computational modeling approach that focuses on modeling individuals as parts of a complex system. There has been an increase in the practical importance of using ABMs in conservation studies, such as in models for the population viability of endangered species and in the management of natural populations (Giacomini 2007; Gotelli 2009). Also, they have been effectively used to simulate the behavior of individual animals in the landscape (Uchmanski and Grimm 1996; Grimm 1999). It is a consensus in the scientific community that more general models lose out in precision, and more accurate models lose out in generalization (Levins 1968). The ABMs are certainly positioned at the extreme of greatest precision and least generality, being, therefore, directed towards the understanding of particular cases, usually used in situations of landscape management and conservation (Giacomini 2007).

The main feature of an ABM is the use of the individual as its primary unit. Thus, in simulation studies in the field of ecology and conservation, a population is no longer represented by a continuous variable, or a state variable, as it is commonly referred in the literature (Jorgensen 1994; Grimm et al. 2006). Individuals are represented explicitly and the rules of the model are directly related to them. It carries as much information as is convenient for the modeling process such as age, sex, or even behavioral characteristics. The location of an individual is monitored across the landscape; in models with an annual time step they can be followed up through an annual cycle of breeding, dispersal and mortality (Pulliam et al. 1992).

Individual-based modeling allows not only the visualization of patterns closer to reality but also a deeper investigation into the mechanisms responsible for such patterns (Huston et al. 1988). Furthermore, individual-based modeling presents a more natural and intuitive logic of representation: the population is, in fact, a collection of discrete entities, or individuals.

Modeling context

The MPSG model

The MPSG (Muriqui Population Spread and Growth) is an individual-based model that simulates movement behavior across the landscape by using population dynamics outputs as a trigger to initiate (and regulate) the events of migration. This model converts information about suitable habitat patch locations, the energetic costs of movement across the matrix and the probability of mortality into information about habitat functional connectivity and its impact on successful migrations among social groups of muriquis. Our model focuses on functional connectivity, that is, on connectivity measured on the basis of both the dispersal characteristics of the species and the landscape structure, rather than considering structural connectivity, which is based solely on the physical features of landscapes (Calabrese and Fagan 2004).

Our algorithm works by creating and launching *virtual animals (VAs)* derived from each group in a specific patch in order to simulate the journey of individuals through a matrix with different types of land cover until they arrive at a different habitat patch (or die). Each one of these *VAs* is given a set rules to follow, derived from the known life history of muriquis. By using a population model as a complement to a habitat model, we were able to improve the predictions of future population demography and distribution and to

forecast the contribution of the social groups within any given patch at the start of the simulation process to the future of the social groups within that same patch.

In the MPSG model, *VAs* move discretely, with a stochastic component, in a chosen direction. Movement can occur within habitat patches or among patches across a variably permeable matrix based on factors that include the costs of moving through non-habitat areas and habitat patch connectivity. A muriqui group in each patch is defined by the number of individuals in the patch. Social groups in each patch are organized as nonmoving infants, juveniles and adults; and moving (but not reproducing) subadult females. Each simulation step (tick) was set to correspond to a time lapse of one year.

Spatial framework and input data

Using the MPSG model, we simulated demographic and individual movement processes over a regular 30 m^2 cell grid, a standard size for satellite imagery commonly used in conservation management assessment. We developed this model using NetLogo, which is a multi-agent programmable and free modeling environment (Wilensky 1999). The experiment was carried out with five social groups of muriquis in the municipality of Santa Maria de Jetibá, state of Espírito Santo (41°02'W – 40 °35'W; 19°56'S – 20°13'S; Figure 3.1), a mountainous Atlantic Forest region in southeastern Brazil (Figure 3.1).

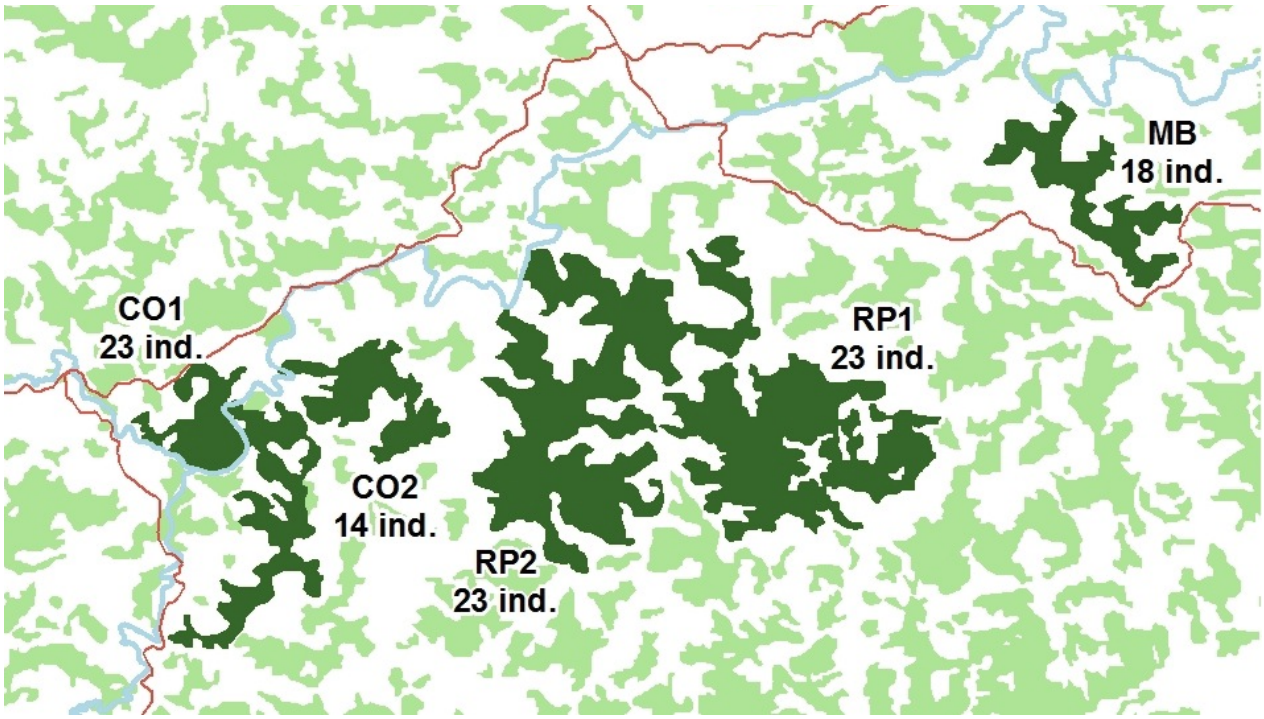


Figure 3.1. Studied area with current distribution of muriqui groups in Santa Maria de Jetibá, ES, Brazil ((MB) Mata do Belém, (RP1 and RP2) Rio das Pedras 1 and 2, (CO1 and CO2) Córrego do Ouro 1 and 2. Blue lines represent rivers and red lines represent main roads.

To account for species-specific habitat considerations in estimating populations and their movement patterns in the landscape, we provided the model with three grid map

inputs with identical geographical extent and cell size: (1) a *habitat map*, with suitable forest patches for muriquis; (2) a *matrix permeability map*, with biological costs for individuals of muriquis to cross non-habitat matrix; and (3) a *mortality map*, which is directly proportional to matrix permeability. These inputs run in parallel to simulate muriqui population dynamics and movements of individuals within each habitat patch occurring in the landscape, providing indications of the potential responses of the muriqui population to landscape structure.

The *habitat map* was generated using simple logistic regressions through Generalized Linear Models to predict the probability of occurrence of muriquis on the basis of the spatial characteristics and connectivity indices of each patch, as described in chapter 1. It is a binary map, with value 0 for non-suitable and value 1 for suitable habitats. The *matrix permeability map* was generated using land use/land cover maps (Centoducatte, 2011) and *ad hoc* interviews with eight specialists in muriqui behavior and ecology (extracted from Santos 2013). Cell permeability values range from 1 to 100 (low to high cost in crossing matrix). The *mortality map* is directly proportional to the matrix costs faced by an individual in crossing the matrix. The greater the cost, the higher the probability that the individual will die. As a relative probability, values were assumed between 0 and 1.

Population dynamics model

To evaluate population dynamics, we used a Leslie model with four stages (i.e. infants, juveniles, subadults and adults) (Figure 3.1). The matrix shown in Figure 3.2 was used to evaluate the population vector consisting of the number of infants, juveniles, subadults and adults for the next time step. We set birth, survival and fecundity probabilities as constant values, dependent only on age class. Life expectancy was set at 37 time steps. Table 3.1 lists the biological parameters of the model that were set for each initialized individual.

Within the muriqui species, males are philopatric and females typically migrate from their natal group when they reach puberty (Printes and Strier 1999; Strier and Ziegler 2000; Strier et al. 2015). For this model, females were able to migrate when age reached six years (i.e. six time steps) and to mate at seven time steps and above. Females in parental care state were unable to reproduce during three time steps. The probability of migration into one of the adjacent cells was calculated on the basis of the biological costs of crossing the matrix through adjacent cells. So, matrix permeability affected the decision and the direction of dispersal of individuals. We applied a chi-square test to compare the model's predictions of population sizes in the presence and in the absence of migration events among groups (i.e. open population (OP) and closed population (CP), respectively).

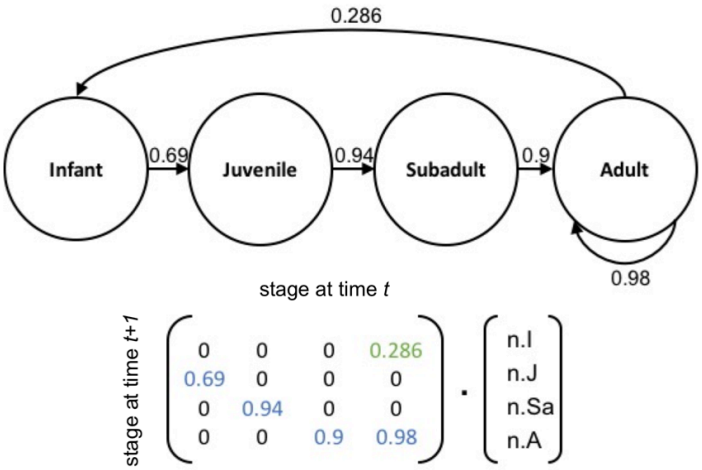


Figure 3.2. Life history diagram and its corresponding Leslie projection matrix for the population of muriquis in Santa Maria de Jetibá, ES, Brazil, with four stages: Infant (n.I), juveniles (n.J), subadults (n.Sa) and adults (n.A). Arrows symbolize probability that individuals in a certain stage will survive and remain in the same stage or pass to the next stage over a time-step. Matrix entries are subdivided into fecundity (green) and survival (blue).

Table 3.1. Parameters used in the simulation. The values employed were estimated on the basis of information obtained in the corresponding references.

Parameter	Value	Reference
Female sexual maturity (years)	7	Strier (1993/1994), updated by Strier in Rylands et al. (1998)
Number of births per female per year	1	Strier et al. (2006)
Number of females breeding per year (%)	28,6 (± 11,4)	Projeto Muriqui - ES
Infant annual mortality (%)	30.9	Bronikowsky et al. (2011)
Juvenile annual mortality (%)	5.59	Bronikowsky et al. (2011)
Subadult annual mortality (%)	10.2	Bronikowsky et al. (2011)
Adult annual mortality (%)	2.25	Bronikowsky et al. (2011)
Longevity (years)	35	Strier (1993/1994), updated by Strier in Rylands et al. (1998)
Sexual rate (males) (%)	45.6	Projeto Muriqui - ES
Dispersal age of females (years)	6	Strier et al. (2006)

Adapted from Lanna 2015.

Process overview

The *starting point* of each group was obtained using the available demographic data (updated from Lanna 2015). These data included the number of individuals in each group, age class and sex. In the simulation, each virtual animal (*VA*) is settled in the patch of the group to which it belongs. Each *VA* moves randomly within its habitat patch and becomes older at each time step. As mentioned above, each time step was equal to one year, during which *VAs* could move randomly within the patch, reproduce and present their dynamics of birth, death and migration to another habitat patch.

All activities, i.e. processes, followed a series of rules, assumptions and defaults (Figure 3.3). A simplified sequence of events is described as follows: (1) when *VA* is ready to travel, the initial direction of travel is chosen randomly; (2) when *VA* reaches the patch edge, it chooses the lowest cost (if present) of three available grid cells; (3) if two or more cells have equal value, the next step is chosen randomly; (4) if all three cells present high cost, *VA* chooses a new direction randomly (from 0 to 360^{o}) and proceeds as in step 2 with a revised general direction; (5) each *VA* can cross a gap of 200 m of matrix between habitat patches; and (6) *VAs* that reach a favorable habitat after migration can survive and reproduce. The iteration process continues for 50 time steps. The following results are then recorded: the number of successful dispersals (the number of times that a *VA* has found another viable patch), population estimates for each group, estimates of migration importance for the population dynamics of each group and the relative importance of the patch (or group) in providing individuals to other patches in the landscape.

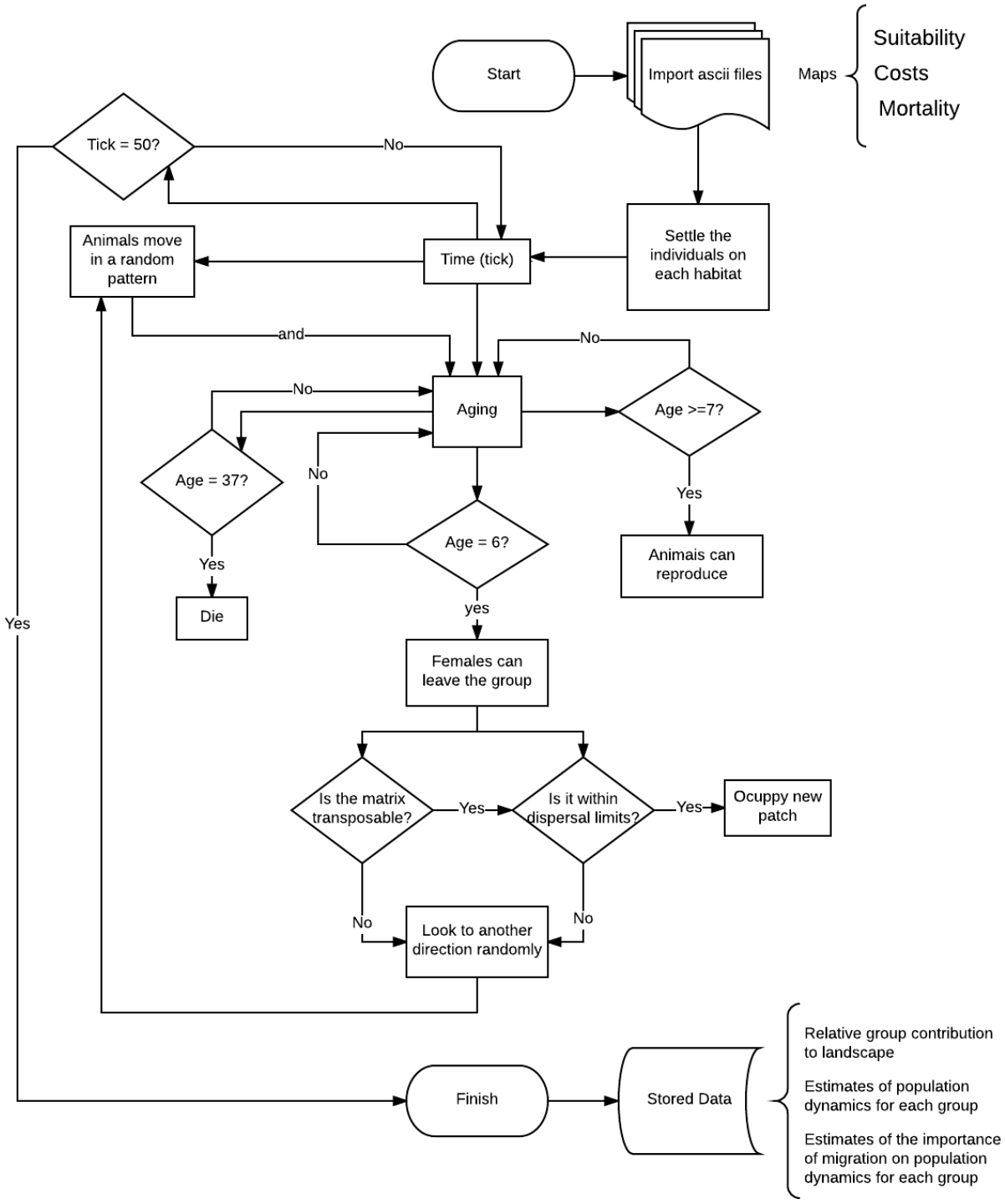


Figure 3.3. Fluxogram of MPSG model (Muriqui Population Spread and Growth). Diamond shapes represent individual decision and rectangle shapes represent action steps.

Results

The ABM simulation of muriquis in SMJ resulted in an average population increase of 2.4-fold in 50 years (from 101 individuals to 248, excluding solitary females). Mean population growth was 2.94 individuals per year. All five groups of muriquis increased in size (Table 3.2, Figure 3.4), whether by mating or spreading of females. Migration played an important role in population growth (X^2=29.25, df=1, p=6.33^{-08}), even if solitary females are excluded (X^2=10.91, df=1, p=0.00095) (Figure 3.5). Table 3.3 displays the distribution of the groups of muriquis and dispersal behavior of females. Females from each group moved within or into other forest fragments and intersperse their groups with other groups.

Table 3.2. Population growth of five social groups of muriquis over a 50 years period in Santa Maria de Jetibá. Initial densities represent real data collected in the field and final density and growth are simulated population dynamics projections that included birth, mortality and migration rates. (MB) Mata do Belém, (RP1 and RP2) Rio das Pedras 1 and 2, (CO1 and CO2) Córrego do Ouro 1 and 2.

Group	Forest fragment Area (ha)	Density (initial) ind/ha	Density (final) ind/ha	Growth ind/year
MB	143	0,13	0,20	0,22
RP1	321	0,07	0,13	0,4
RP2	442	0,05	0,13	0,66
CO1	151	0,15	0,40	0,74
CO2	77	0,18	0,78	0,92

The values obtained from the MPSG model suggest that MB is virtually isolated from the other groups (no input from or output to other groups), indicating a potential for genetic drift and inbreeding. MB shows a contribution of only four females to the landscape, and all of them become solitary in adjacent forest patches with no groups of muriquis. Conversely, CO1 and CO2 appear to have the strongest connectivity to other patches. Together they contribute with almost 60% of females dispersing to neighboring forest patches. Even though CO1 and CO2 are patches with intermediate sizes, both patches and their most important neighbors (e.g. patches 11, 21 and 71) are important to ensure population persistence in the future. RP1 and RP2 represent larger areas, with intermediate connectivity among patches and contribute with 36% of the females that spread through the landscape.

Out of 73 females that dispersed, only 28 settled in a different group of muriquis. The model indicates that 45 dispersing females could not migrate to another established group of muriquis and would become solitary in a neighboring forest patch.

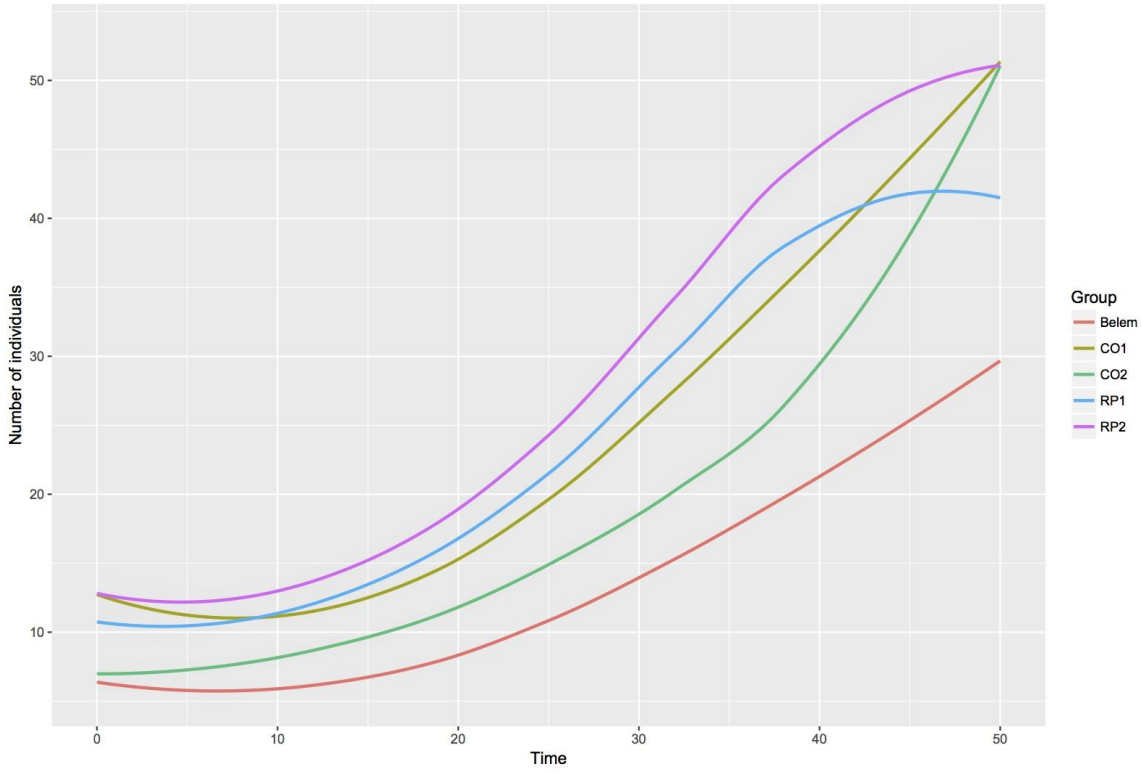


Figure 3.4. Estimates of population growth using Leslie matrix for five social groups of muriquis over a 50 years period in Santa Maria de Jetibá, ES, Brazil. Data are presented without emigration events (i.e. as if each group was considered as a closed population). (MB) Mata do Belém, (RP1 and RP2) Rio das Pedras 1 and 2, (CO1 and CO2) Córrego do Ouro 1 and 2.

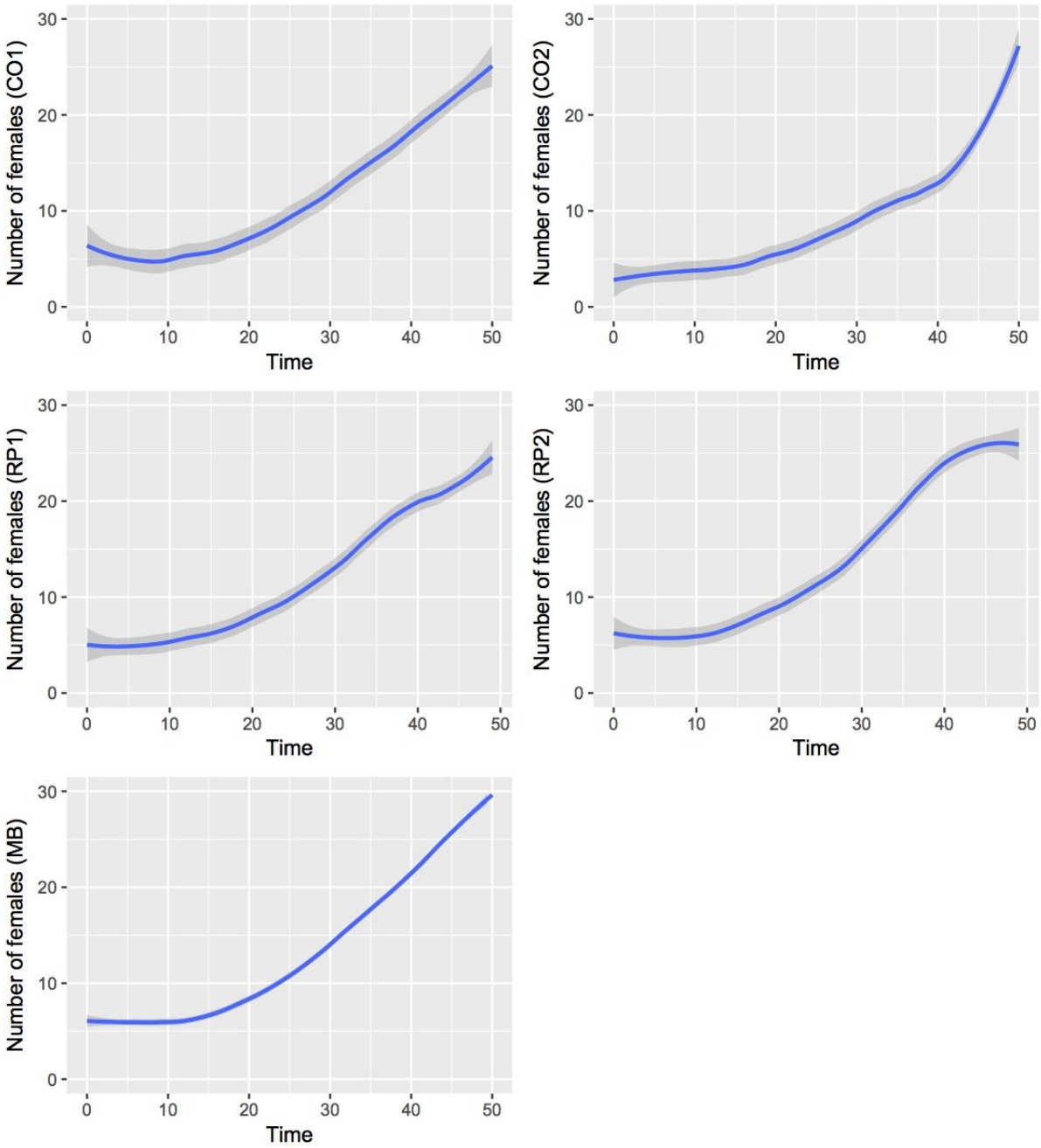


Figure 3.5. Estimates of population growth using MPSG model, a spatially-explicit agent-based model, for five social groups of muriquis over a 50 years period in Santa Maria de Jetibá, ES, Brazil. Blue lines represent group growth considering birth and mortality rates and gray bands represent the conditional mean of potential contribution of individuals through dispersal events. As only muriqui females migrate from their natal group, growth data are shown only for females. For total group sizes, see Table 3.3. (MB) Mata do Belém, (RP1 and RP2) Rio das Pedras 1 and 2, (CO1 and CO2) Córrego do Ouro 1 and 2.

Table 3.3. Distribution of five groups of muriquis and dispersal behavior of females in Santa Maria de Jetibá, ES, Brazil. Columns 1–4 show the original areas followed by initial and final group sizes (CP, closed population and OP open population, respectively). The remaining columns show the distribution of individuals within each forest patch with lineages originating from the areas indicated by the column headings. Bold values mark the row-column intersections associated with the same area.

Area	Start Individuals	End individuals (CP)	End individuals (OP)	Patches																													
				MB	RP1	RP2	CO1	CO2	73	16	84	61	48	44	69	70	87	88	65	75	71	70	56	24	26	43	21	15	11	19	67
MB	18	29	29	**29**	0	0	0	0																							
RP1	23	37	43	0	**37**	2	3	1																							
RP2	23	49	56	0	3	**49**	1	3																							
CO1	23	51	60	0	2	2	**51**	5																							
CO2	14	54	60	0	1	1	4	**54**																							
73	0	0	3	3	0	0	0	0	**0**																						
16	0	0	1	1	0	0	0	0	0	**0**																					
84	0	0	2	0	2	0	0	0	0	0	**0**																				
61	0	0	1	0	1	0	0	0	0	0	0	**0**																			
48	0	0	2	0	2	0	0	0	0	0	0	0	**0**																		
44	0	0	2	0	2	0	0	0	0	0	0	0	0	**0**																	
69	0	0	2	0	0	2	0	0	0	0	0	0	0	0	**0**																
70	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	**0**															
87	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	**0**														
88	0	0	3	0	0	3	0	0	0	0	0	0	0	0	0	0	0	**0**													
65	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	**0**												
75	0	0	2	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	**0**											
71	0	0	4	0	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	**0**										
70	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**									
56	0	0	2	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**								
24	0	0	2	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**							
26	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**						
43	0	0	2	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**					
21	0	0	3	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**				
15	0	0	2	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**			
11	0	0	3	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**		
19	0	0	2	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	
67	0	0	2	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
TOTAL	101	220	293																												
Patch contribution of ind. to landscape (observed)				4	13	13	22	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Patch contribution of ind. to landscape (relative)				0,05	0,18	0,18	0,30	0,29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Discussion

The MPSG model

The development of the MPSG model was motivated by the need to understand the future spatial distribution of the muriqui population in SMJ and to contribute to the operational conservation planning in order to ensure the persistence of this species in the landscape. Even though we conducted the simulations considering the spatial configuration of the highly patchy SMJ landscape, this model is useful for evaluating the importance of habitat patches and dispersal paths for muriquis in any landscape within their historical distribution.

Although our MPSG model is very simple, it was technically sufficient to capture the essential elements of real world migrations for the muriqui species. Simpler analytical approaches are possible, such as the least-cost method for predicting migration paths, but they do not take into account many essential aspects of animal ecology and behavior (Hargrove and Westervelt 2012). The *VAs* in the simulation, considered individually, have almost no sophistication in finding migration paths as compared with individuals in the real world. However, considered collectively, the behavior of all successful *VAs* constitutes a spatial optimization process that can be used to reproduce the optimum pathways we would expect individual muriquis to use most often.

Using the available demographic data about the muriqui population in SMJ (birth, growth and mortality rates), we were able to describe the development of individuals throughout their life cycles. The response of these rates to environmental variations along with emigration and immigration rates determined population dynamics and could explain changes in population size and composition (Caswell 1989). The life history tables for each social group helped us to understand the population dynamics of muriquis, integrating the data of fertility and survival of each stage of the life cycle, thus allowing the calculation of the parameters of population growth and life expectancy by specific age (Southwood 1978; Rockwood 2006). The growth of populations classified by age classes and life stages was projected over time using matrix algebra. The Leslie matrix is a tool that assumes that individuals in each age group or stage of life are subject to fertility and mortality rates that remain constant over time (Leslie 1945).

The population of muriquis in SMJ

Our model indicates that all muriqui groups found in Santa Maria de Jetibá are viable for the next 50 years, although their long term viability is uncertain. The importance of large habitat patches to population viability, such as the RP forest complex, is obvious and not surprising. Larger habitat patches are likely to host more individuals, including colonizers and dispersing breeders (Fahrig and Paloheimo 1988; Clobert et al. 2009). Nevertheless, connectivity among habitat patches, such as in the CO forest complex, also plays an important role in ensuring species persistence, corroborating the results in chapter 1, in which the occurrence of muriquis was associated with regions of higher forest growth rates and connectivity. CO1 and CO2, along with their most important neighbors, are not the biggest patches in the landscape. However, together they contribute to the majority of females that dispersed through the landscape and constitute perhaps the most important

area for conservation and to ensure population persistence in the future. In fact, connectivity may be as important as (or even more important than) habitat size, especially for species with dispersal process (Urban and Keitt 2001).

At the population level, immigration leads to higher population growth in patches with social groups. For the muriquis, migration paths can be made of *stepping stones* separated by distances no greater than the greatest size of non-habitat matrix areas they are able to cross, in order to overcome the habitat isolation resulting from the heterogeneity of the landscape's spatial configuration. With the dispersion of females, the reproductive success, at every time step, introduces in the population new individuals that can also reproduce and gradually increase the genetic variability within the population. However, we found that in SMJ only 38% of the dispersing females will encounter a known group of muriqui, while the other 62% will probably have no success in finding a mating partner because their dispersal will lead to empty patches. Also, we found that one group, the MB, is completely isolated, being therefore the most susceptible to local extirpation due to decreases in population abundance and genetic diversity (Goossens et al. 2005; Chaves et al. 2011).

Our simulation suggests that the social groups of muriquis in SMJ are arranged as a spatially structured population (SSP), composed of patches of breeding habitats holding local social groups which are interconnected by dispersing individuals (Thomas and Kunin 1999). This dynamics is the result of processes at the level of individuals. The system in SMJ shows both metapopulation properties (Hanski 1998) and source-sink dynamics (Pulliam 1988). However, we still lack explicit data to consolidate both hypotheses.

In SMJ, the groups of muriquis can be considered as parts of a metapopulation in which immigrants from one group are likely to found another social group in a different forest patch, thus ensuring biological flow within the population (Levins 1969; Hanski 1998). Except for the MB group, all groups of muriquis contributed with dispersal females among them. They also contributed with females to empty neighboring patches. As local extinctions and recolonization occur over time, not necessarily all suitable patches will be occupied and empty habitats left empty by the extinction of a group could be recolonized.

In source-sink dynamics, patches working as a sink for a population are a very serious issue for local species conservation, especially threatened ones. In our study area, MB may work as a sink patch; the same seems to occur for suitable forest patches that are empty or with solitary females. Females at dispersal age within the MB group have a great chance to become solitary in smaller patches close to the source patch. Therefore, it is likely that in the future MB will not contribute to the lineages of muriquis in the region. Sink subpopulations inhabit relatively poor quality habitats and will eventually become extinct if they do not receive influx of immigrants from other subpopulations (Brown and Kodric-Brown 1977; Pulliam 1988; Donovan et al. 1995).

For conservation management, we should consider two scenarios for sink patches: connectivity and/or translocation. In both scenarios the goal is to preserve the genetic information of the subpopulations (Seddon 2010; Rayfield et al. 2011). However, the results would be completely different for the MB group. Translocation would mean to dissolve the subpopulation through capture and to release individuals from MB into other groups in the landscape. Connectivity, on the other hand, involves the preservation of the subpopulations, but allowing a flux of immigrants. To implement a conservation plan using

one of these two scenarios, it is necessary to consider their viability, both biologically and economically.

Managers and planners are increasingly seeking decision support tools based on simulation modeling to help assess the impacts of development alternatives (Jorgensen et al. 1996; van Daalen et al. 2002). A significant number of models have been developed for understanding the process of fragmentation and its effects. The use of population models as complements to habitat models could improve predictions of species-specific demographic responses to environmental changes (BenDor et al. 2009).

For endangered species with special restrictions in their dispersal ranges and in the kinds of habitats through which they can disperse, factors such as the spatial configuration of the landscape and species-specific practical conservation issues can only be known from studies of real populations in real landscapes (Hobbs 1992). However, there is still a need to couple empirical studies with theoretical models in the proper investigation of the implications of spatial heterogeneity on population distribution and species persistence (Johnson et al. 1992, Tischendorf and Wissel 1997).

Conclusions and future perspectives

Our results show that female migration plays an important role in muriqui population growth, indicating the remarkable effect of patch connectivity in the spread of population. Real data collected in the field (see chapter 2) confirm that some females risk crossing non-habitat area when dispersing. Our simulation with the MPSG model shows that forest patches in SMJ, despite being mostly smaller than 200 ha, are close enough to ensure typical dispersal behavior to occur at least for one third of the females in known social groups.

The simulation corroborates the conceptual model developed in chapter 2, which indicates that fragmentation alters the muriquis's patterns of movement and dispersal across landscapes. Isolated forest patches (e.g. Mata do Belém) produced a complete change in the typical behavior of muriquis while forest patches functionally connected (e.g. Córrego do Ouro 1 and 2) preserved that typical behavior. The combination of population demography information, life history of individuals and landscape data on habitat fragmentation can extend our plan, improving conservation and management and insuring that in the future there will be females of this species able to disperse, even beyond the 50 years time lapse simulated in this chapter.

As we pointed out in chapter 1, patch size and forest growth were also found to influence the distribution of muriquis. So, the regeneration of the forest cover along time should be taken into account in trying to understand how landscape dynamics influences the present muriqui population distribution, and how it is important in evaluating the landscape in the conservation of an endangered species. In fact, our next step is to improve the MPSG model by incorporating a carrying capacity factor to regulate population spread and growth; and a landscape change model based on local economic variations in order to predict different scenarios and the potential of habitat management for population recovery.

For conservation purposes, models that estimate the spatial behavior of populations in the landscape, including spatial and population information, provide useful insights on how they can be maintained to avoid future losses and local extinctions of species. Although our model can be very helpful in revealing potential population responses to landscape configuration, it is still incapable of predicting variations in population dynamics when the rates of birth, survival and fecundity are not constant probabilities. Nonetheless, a spatially explicit individual-based model can be a powerful intuitive tool to understand how past landscape features shaped present species distribution and to project the future persistence of this species.

References

BenDor T, Westervelt J, Aurambout JP, Meyer W. 2009. Simulating population variation and movement within fragmented landscapes: An application to the gopher tortoise (*Gopherus polyphemus*). Ecological Modelling 220(6): 867-878.

Bengtsson BO. 1978. Avoiding inbreeding: at what cost? J. theor. Biol. 73: 439–444.

Brito D, Grelle CEV. 2006. Estimating Minimum Area of Suitable Habitat and Viable Population Size for the Northern Muriqui (*Brachyteles hypoxanthus*). Biodiversity Conservation 15: 4197–4210.

Brito D, Grelle CEV, Boubli JP. 2008. Is the Atlantic Forest protected area network efficient in maintaining viable populations of *Brachyteles hypoxanthus*? Biodiversity Conservation 17: 3255–3268.

Bronikowski AM, Altmann J, Brockman DK, Cords M, Fedigan LM, Pusey A, Stoinski T, Morris WF, Strier KB, Alberts SC. 2011. Aging in the natural world: comparative data reveal similar mortality patterns across primates. Science 331: 1325–8.

Brown JH, Kodric-Brown A. 1977. Turnover Rates in Insular Biogeography: Effect of Immigration on Source. Ecology 58(2): 445-449.

Calabrese JM, Fagan WF. 2004. A comparison-shopper's guide to connectivity metrics. Frontiers in Ecology and the Environment 2(10): 529-536.

Carter N, Levin S, Barlow A, Grimm V. 2015. Modeling tiger population and territory dynamics using an agent-based approach. Ecological Modelling 312: 347-362.

Caswell H. 1989. Matrix Population Models: Construction, Analysis, and Interpretation, 1st ed. Massachusetts, Sinauer Associates, Inc. Publishers Sunderland, 328 p.

Centoducatte LD. 2011. Fragmentação da Mata Atlântica e conservação do muriqui-do-norte, *Brachyteles hypoxanthus* (Primates, Atelidae). Master Thesis.

Chaves PB, Alvarenga CS, Possamai CDB, Dias LG, Boubli JP, Strier KB, ... & Fagundes V. 2011. Genetic diversity and population history of a critically endangered primate, the northern muriqui (*Brachyteles hypoxanthus*). PloS one, 6(6): e20722.

Clobert J, Galliard L, Cote J, Meylan S, Massot M. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecology letters 12(3): 197-209.

Cushman SA. 2006. Effects of habitat loss and fragmentation on amphibians: a review and prospectus. Biological conservation 128(2): 231-240.

Dias LG, Strier KB. 2003. Effects of group size on ranging patterns in *Brachyteles arachnoides hypoxanthus*. International Journal of Primatology 24(2): 209-221.

Doerr VA, Barrett T, Doerr ED. 2011. Connectivity, dispersal behavior and conservation under climate change: a response to Hodgson et al. Journal of Applied Ecology 48(1): 143-147.

Donovan TM, Clarke DA, Howe RW, Danielson BJ. 1995. Metapopulations, sources and sinks, and the conservation of neotropical migratory birds in the midwest. In: Management of midwestern landscapes for the conservation of neotropical migratory birds. Thompson, F.R., III (ed). St Paul: US Forest service, North Central Forest Experiment Station, GTR_NC-187, p.41.

Eduardo AA, Brito D. 2012. The impacts of population subdivision on the viability of *Brachyteles hypoxanthus*. Folia Primatol. 83: 76–84.

Fahrig L, Merriam G. 1994. Conservation of fragmented populations. Conservation biology 8(1): 50-59.

Fahrig L, Paloheimo J. 1988. Effect of spatial arrangement of habitat patches on local population size. Ecology 69(2): 468-475.

Fleishman E, Ray C, Sjögren-Gulve P, Boggs CL and Murphy DD. 2002. Assessing the roles of patch quality, area, and isolation in predicting metapopulation dynamics. Conservation Biology 16(3): 706-716.

Gehring TM, Swihart RK. 2003. Body size, niche breadth, and ecologically scaled responses to habitat fragmentation: mammalian predators in an agricultural landscape. Biological conservation 109(2): 283-295.

Giacomini HC. 2007. Sete motivações teóricas para o uso da modelagem baseada no indivíduo em ecologia. Acta Amazonica 37(3): 431-446.

Goossens B, Chikhi L, Jalil MF, Ancrenaz M, Lackman-Ancrenaz I, Mohamed M, ... & Bruford, M. W. 2005. Patterns of genetic diversity and migration in increasingly fragmented and declining orang-utan (*Pongo pygmaeus*) populations from Sabah, Malaysia. Molecular Ecology 14(2): 441-456.

Gotelli NJ. 2008. A Primer of Ecology, 4th ed., Sinauer Associates, Inc., Sunderland, Massachusetts.

Grimm V. 1999. Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? Ecological modelling 115: 129-148.

Grimm V, Berger U, Bastiansen F, Eliassen S, Ginot V, Giske J., ... and Huth A. 2006. A standard protocol for describing individual-based and agent-based models. Ecological modelling 198(1): 115-126.

Hanski I. 1998. Metapopulation dynamics. Nature 396: 41–49.

Hargrove WW, Westervelt JD. 2012. An Implementation of the Pathway Analysis Through Habitat (PATH) Algorithm Using NetLogo. In Ecologist-Developed Spatially-Explicit Dynamic Landscape Models (pp. 211-222). Springer US.

Huston M, DeAngelis DL, Post W. 1988. New computer models unify ecological theory. Computer simulations show that many ecological patterns can be explained by interactions among individual organisms. BiosScience 38: 682-691.

ICMBio. 2011. Plano de Ação Nacional para a Conservação dos Muriquis. (org) Jerusalinsky L, Talebi M, de Melo FR. Brasilia, DF. 143p.

ICMBio. 2016. Brazil Red Book of Threatened Species of Fauna. Brasilia, DF. 75pp.

IPEMA. 2007. Espécies da fauna ameaçadas de extinção no Estado do Espírito Santo. (org) Passamani P., Mendes SL. Vitória, ES.

IUCN 2016. IUCN Red List of Threatened Species. <www.iucn.org>. Access: July 2016.

Jorgensen SE. 1994. Fundamentals of ecological modeling. 2ª ed. Elsevier Science B.V

Keesen F, Silva AC, Arashiro E and Pinheiro CFS. 2017. Simulations of populations of *Sapajus robustus* in a fragmented landscape. Ecological Modelling 344: 38-47.

Lanna AM. 2015. Viabilidade populacional do Muriqui-do-Norte, *Brachyteles hypoxanthus* (Kuhl, 1820) em área fragmentada. Master Thesis.

Leslie PH. 1945. On the use of Matrices in Certain Population Mathematics. Biometrika 33: 183-212.

Levins R. 1968. Evolution in Changing Environments - some theoretical explorations. 1ª ed. Princeton University Press, Princeton.

Liao J, Li Z, Hiebeler DE, Iwasa Y, Bogaert J, Nijs I. 2013. Species persistence in landscapes with spatial variation in habitat quality: a pair approximation model. Journal of theoretical biology 335: 22-30.

Lindenmayer DB, Fischer J, Felton A, Crane M, Michael D, Macgregor C, ... Hobbs RJ. 2008. Novel ecosystems resulting from landscape transformation create dilemmas for modern conservation practice. Conservation Letters, 1(3): 129-135.

Martensen AC, Pimentel RG, Metzger JP. 2008. Relative effects of fragment size and connectivity on bird community in the Atlantic Rain Forest: implications for conservation. Biological Conservation 141(9): 2184-2192.

Mendes SL, Melo FR, Boubli JP, Dias LG, Strier KB, Pinto LPS, ... and De Marco Jr P. 2005a. Directives for the conservation of the northern muriqui, *Brachyteles hypoxanthus*. Primates, Atelidae. Neotrop Primates 13: 7-18.

Mendes SL, Santos RR, Carmo, LR. 2005b. Conserving the northern muriqui in Santa Maria de Jetiba, Espirito Santo. Neotrop Primates 13(Suppl):31–35.

Mittermeier RA, Valle CMC, Alves MC, Santos IB, Pinto CAM, Strier KB, Young AL, Veado EM, Constable ID, Paccagnella SG, Lemos de Sá RM. 1987. Current distribution of the muriqui in the Atlantic forest region of Eastern Brazil. Primate Cons. 8:143–149.

Moilanen A, Hanski I. 2001. On the use of connectivity measures in spatial ecology. Oikos, 95(1): 147-151.

Pinto LPS, Costa CMR, Strier KB, Fonseca GAB. 1993. Habitat, density and group size of primates in a Brazilian tropical forest. Folia Primatologica 61: 135-143.

Printes RC, Strier KB. 1999. Behavioral correlates of dispersal in female muriquis (*Brachyteles arachnoides*). Int J Primatol 20:941–960.

Pulliam HR. 1988. Sources, sinks, and population regulation The American Naturalist 132 (5), 652-661.

Pulliam HR, Dunning JB, Liu J. 1992. Population dynamics in complex landscapes: a case study. Ecological Applications 2 (2): 165-177.

Rayfield B, Fortin MJ, Fall A. 2011. Connectivity for conservation: a framework to classify network measures. Ecology 92(4): 847-858.

Rockwood LL. 2006. Populations with age structures p. 77-107. In: Introduction to Population Ecology. Blackwell Publishing.

Rylands AB, Strier KB, Mittermeier RA, Borovansky J, Seal US. 1998. Population and Habitat Viability Assessment (PHVA) for the muriqui (*Brachyteles arachnoides*), CBSG. Belo Horizonte.

Santos BS. Modelos de Dispersão Populacional do muriqui-do- norte, *Brachyteles hypoxanthus* (Primates, Atelidae). Master thesis.

Seddon PJ. 2010. From reintroduction to assisted colonization: moving along the conservation translocation spectrum. Restoration Ecology 18(6): 796-802.

Söndgerath, D, Schröder B. 2002. Population dynamics and habitat connectivity affecting the spatial spread of populations–a simulation study. Landscape Ecology 17(1): 57-70.

Southwood TRE. 1978. The construction, description and analysis of age-specific life- tables. In: Ecological Methods with Particular Reference to the Study of Insect Population. London, Chapman & Hall.

Strier KB. 1993/1994. Viability analyses of an isolated population of muriqui monkeys (*Brachyteles arachnoides*): implications for primate conservation and demography. Primate Conservation 14-15: 43-52.

Strier KB. 2000. Population viability and regional conservation priorities for muriquis (*Brachyteles arachnoide*s) in Brazil's Atlantic forest. Biotropica 32(4b): 903-913.

Strier KB, Ziegler TE. 2000. Lack of pubertal influences on female dispersal in muriqui monkeys, *Brachyteles arachnoides*. Anim Behav 59(4):849–860.

Strier KB, Boubli JP, Possamai CB, Mendes, L. 2006. Population Demography of Northern Muriquis (*Brachyteles hypoxanthus*) at the Estação Biológica de Caratinga / Reserva Particular do Patrimônio Natural-Feliciano Miguel Abdala, Minas Gerais, Brazil 237, 227–237.

Strier KB, Possamai, CB, Mendes SL. 2015. Dispersal Patterns of Female Northern Muriquis: Implications for Social Dynamics, Life History, and Conservation. (Eds) Takeshi F., Yamagiwa J, Aureli F. In: Dispersing Primate Females: Life History and Social Strategies in Male-Philopatric Species. Primatology Monographs. pp 3-22.

Swart J, Lawes MJ. 1996. The effect of habitat patch connectivity on samango monkey (*Cercopithecus mitis*) metapopulation persistence. Ecological Modelling 93(1-3): 57-74.

Thomas CD. 1994. Extinction, colonization, and metapopulations: environmental tracking by rare species. Conservation Biology 8(2): 373-378.

Thomas CD, Kunin WE. 1999. The spatial structure of populations. J Anim Ecol 68:647–657.

Tischendorf L, Wissel C. 1997. Corridors as Conduits for Small Animals: Attainable Distances Depending on Movement Pattern, Boundary Reaction and Corridor Width. Oikos 79(3): 603-611.

Uchmanski J, Grimm V. 1996. Individual-based modelling in Ecology: what makes the difference? Trends in Ecology and Evolution 11: 437-441.

Uezu A, Metzger JP, Vielliard JM. 2005. Effects of structural and functional connectivity and patch size on the abundance of seven Atlantic Forest bird species. Biological Conservation 123(4): 507-519.

Urban D, Keitt T. 2001. Landscape connectivity: a graph-theoretic perspective. Ecology 82(5): 1205-1218.

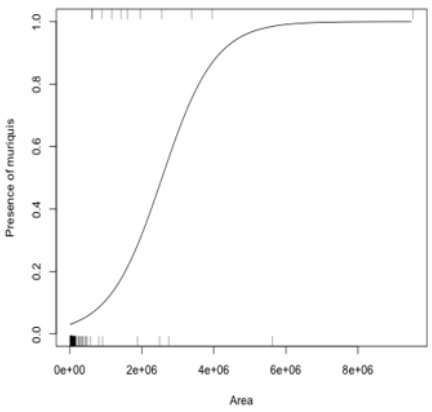
Van Daalen CE, Dresen L, Janssen MA. 2002.The roles of computer models in the environmental policy life cycle. Environmental Science & Policy 5(3): 221-231.

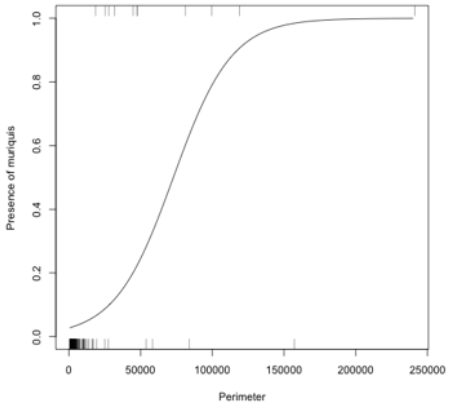
Wilensky U. 1999. Netlogo. Northwestern University Center for Connected Learning and Computer-based Modeling, Evanston, IL.

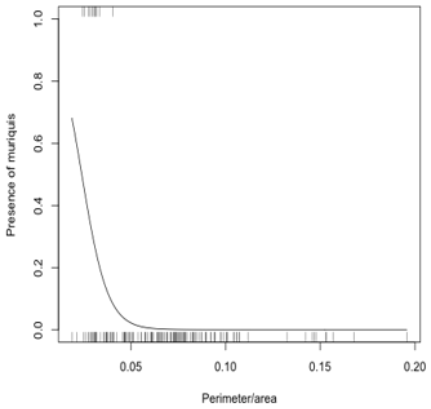
Anexos

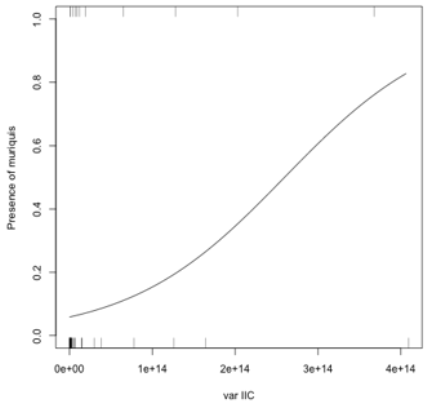
Anexo A

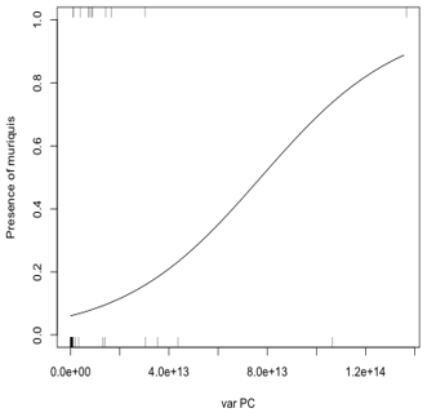
Muriquis occurrence as function of variables of 2008 estimated by simple logistic regressions in chapter 1

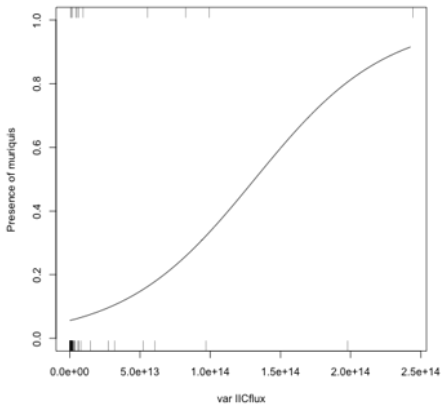


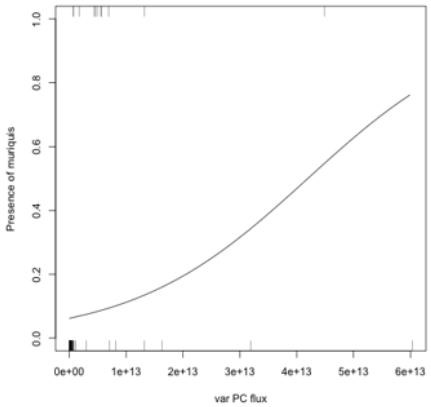












Anexo B

Source code of the MPSG model (Muriqui Population Spread and Growth) developed in Chapter 3

```
#allow to load extensions

extensions [ gis array ]

#create and define variables; patches are assigned a unique ID; count steps of movement; keep track of how many muriquis successfully moved from one patch to another; and list all patches with high quality.

globals [
  total-habitats
  steps
  success-cross
  good-fragments
]

#create and define variables related to the landscape; quality, unique patch id, energetic cost to cross the matrix, probability of a muriqui dying; and a log of VAs that crossed from one patch to another.

patches-own [
  quality
  tagged
  habitat-ID
  cost-energetic
  lethality
  crossed
  ]

breed [ muriquis muriqui ]

muriquis-own [
  habitat-initial
  habitat-actual
  total-steps
  fragment-initial
  lista-of-fragments
  energy
]

breed [ habitats habitat ]
```

```
habitats-own [
  ID
  extent
  edge-patches
]

#creation of VAs and spatial positioning of them in each group

to initialize-muriquis
  random-seed new-seed

  create-muriquis 12 [setxy -19 4] # RP2
  create-muriquis 11 [setxy 33 16] # Belém
  create-muriquis 11 [setxy 23 -1] # RP1
  create-muriquis 8 [setxy 3 -4]   # CO1
  create-muriquis 7 [setxy -6 3]   # CO2

end

#Start the dynamics of movement

to go
  tick
  ask muriquis
  [
    set fragment-initial new-fragment-initial
    set habitat-initial  [habitat-ID] of fragment-initial
    set total-steps 0
    set list-of-fragments []
    #if fragment-initial != NOBODY [
    move-to fragment-initial
  ]
    set pcolor black
    set energy energy-initial
    let my-neighbors neighbors with [ quality <= 1 ]
    if count my-neighbors > 0
    [
    face one-of my-neighbors
    while [ energy > 0 ]
    [
      rt (random Angle-maximum-turn)
      lt (random Angle-maximum-turn)
      forward 1
      ifelse ( habitat-ID = NOBODY )
      [
```

```
#On each tick the VA record the initial patch and classifies each
available surrounding cells one as good or bad pixels, based on
proximity, lethality and type of matrix.

set list-of-fragments lput patch-here list-of-fragments
        set energy energy - cost-energetic
        if (random-float 100) < lethality [ set energy 0 ]
      ]
      [
if ( habitat-initial != habitat-ID )
        [
          foreach list-of-fragments
          [ [?1] ->
            ask ?1
            [
              set crossed crossed + 1
              set pcolor black
            ]
          ]
          increment-travel-success fragment-initial patch-here
        ]
        set energy 0
      ]
    ]
    ]
  ]
end

to increment-travel-success [ start-patch end-patch ]
  let index ( ( ( [ID] of [habitat-ID] of start-patch ) - 1 ) *
total-habitats ) + ( [ID] of [habitat-ID] of end-patch - 1)
  array:set success-cross index  ( array:item success-cross index + 1
)
end

to-report get-travel-success [ start-habitat end-habitat  ]
  let index ( ( start-habitat - 1 ) * total-habitats ) + ( end-
habitat - 1)
  report array:item success-cross index
end

to-report new-fragment-initial
  let tmp [habitat-ID] of one-of good-fragments
  report one-of [edge-patches] of tmp
end

#Import the ascii files with spatial data
```

```
to initialize

__clear-all-and-reset-ticks

 let dataset gis:load-dataset
"/suitable.asc" suitable

  type gis:width-of dataset
  type " colunas e "
  type gis:height-of dataset
  print " linhas."

gis:apply-raster gis:load-dataset
"/cost.asc" cost-energetic

gis:apply-raster gis:load-dataset
"/lethality.asc"   lethality

initialize-muriquis

set-extents
initialize-habitats
set good-fragments patches with [ quality <= 10 ]

end

#calculations to find and define suitable (good) areas

to set-extents
  ask patches [ set tagged FALSE]
  set total-habitats 0
  let y min-pycor
  while [ y <= max-pycor ]
  [
    let x min-pxcor
    while [ x <= max-pxcor ]
    [
      ask patch x y [ find-extent ]
      set x x + 1
    ]
    set y y + 1
  ]
  ask patches [ if habitat-ID = 0 [ set habitat-ID NOBODY ]]
end


to find-extent
  if ( habitat-ID != 0 OR quality != 1 ) [ stop ]
```

```
  if ( habitat-ID != 0 OR quality != 1 OR quality != 10  ) [ stop ]
  set total-habitats total-habitats + 1
  sprout-habitats 1 [ set ID total-habitats ]
  let the-habitat one-of habitats with [ ID = total-habitats ]
  tag-neighbors SELF quality
  let the-count count patches with [ tagged = TRUE ]
  ask the-habitat [ set extent the-count ]
  ask the-habitat [ set plabel ID set plabel-color black ]
  ask patches with [ tagged = TRUE ] [ set habitat-ID the-habitat
set tagged FALSE ]
end

to tag-neighbors [ start-patch qual ]
  let tag-list (list start-patch)
  let at-patch 0
  ask start-patch [ set tagged TRUE ]
  while [ ( length tag-list ) > 0 ]
  [
    let cur-patch first tag-list
    set tag-list butfirst tag-list
    ask cur-patch
    [
       set tag-list lput (neighbors7 with [ habitat-ID = 0 AND tagged
= FALSE AND quality = qual ] ) tag-list #
       ask neighbors7 with [ habitat-ID = 0 AND tagged = FALSE AND
quality = qual ] [ set tagged TRUE ]
    ]
  ]
  write-to-file
end

To population-dynamics

Set initial-population self each-path
for each tick
  ask turtles age
  while age < 37 [age+1]
    if age = 6 start-dispersal
  While age < 36 reproduce
    if age = 37 die
  else age >= 7 sprout +1

import module mathematica

Set leslie-matrix
Input data '/muriquis.txt'
run
report projection-matrix
```

```
end

#calculations to find how many VAs have successfully crossed the
matrix

to initialize-habitats
success ID
  set success-cross    array:from-list n-values ( total-habitats *
total-habitats ) [ 0 ]

  ask habitats
  [
    let tmp self
    set edge-patches patches with [ habitat-ID = tmp ]
    set edge-patches edge-patches with [ count neighbors with [
habitat-ID = tmp ] <= 7 ]                          #
    ask edge-patches [ set pcolor green ]
  ]
end

to print-output
  ##print good-fragments
  print habitat-ID
end

#define biological characteristics of muriquis

to setup

 set age 0
 set reproductive-age 7
 set end-reproductive-age 36
 set age-death 37
 set age-of-dispersal 6
 set annual-mortality-adults 1.25

reset-ticks

end

#adjusts and prepare outputs to be recorded as text files

let file user-new-file
if is-string? file
  [
    file-open file
    write-to-file
```

```
  ]
end

to write-to-file
  file-print (word “---------- Tick Number: “ ticks “----------“
initial-fragment ---------- “ actual-fragment ---------- “ number-of-
females ----“ total-number ------ “)

  foreach sort turtles [ [?1]
    ask ?1 [
      file-print (word self ": pxcor: " pxcor " pycor: " pycor "
value: " habitat-ID )
      file-print(success-cross)
    ]
  ]
  file-print ""
  blank line

end
```